Ecological Monographs, 77(4), 2007, pp. 545–568

LONG-TERM DATA REVEAL COMPLEX DYNAMICS IN GRASSLAND IN RELATION TO CLIMATE AND DISTURBANCE

Richard J. Hobbs,[1,3] Susan Yates,[1] and Harold A. Mooney[2]

[1]*School of Environmental Science, Murdoch University, Murdoch, Western Australia 6150 Australia*
[2]*Department of Biological Sciences, Stanford University, Stanford, California 94305 USA*

Abstract. We conducted a long-term experiment in grassland with the aim of elucidating grassland dynamics in relation to variations in rainfall amount and spatial and temporal variation in disturbance. In particular we aimed to increase our understanding of ecosystem dynamics and function, species redundancy, invasion biology, and other related topics. We studied the dynamics of serpentine annual grassland in northern California over the period 1983–2002 in a replicated series of experimental plots comprising controls, gopher exclosures, and aboveground herbivore exclosures. Annual rainfall amount varied greatly during the study period, which included two major El Niño events and a period of prolonged below-average rainfall. Gopher disturbance was highly variable both spatially and temporally but was positively correlated with soil depth. Disturbance was reduced but not eliminated from the gopher exclosures and was significantly increased in the aboveground herbivore exclosures. Grassland dynamics were driven by rainfall amounts and distributions that had the most pronounced effects on the dominant plant species, while gopher disturbance had additional effects on the rarer species. Effects of excluding aboveground herbivores were swamped by a large increase in gopher disturbance within aboveground exclosures. Overall species numbers were reduced during a period of below-average rainfall but recovered in subsequent years. There was a large array of different responses of individual plant species to both rainfall and disturbance. Our results provide support for the "insurance" hypothesis, which suggests that biodiversity buffers ecosystem processes against environmental changes because different species (or phenotypes) respond differently to these changes, leading to functional compensations among species. Here, a species that was at very low abundance levels at the start of the study (*Microseris douglasii*) temporarily increased in abundance to become one of the dominant species in the grassland following a period of prolonged below-average rainfall. We also observed the repeated invasion of the serpentine grassland by the nonnative grass *Bromus hordeaceus*, which increased greatly in abundance following both of the major El Niño events. The results emphasize the importance of long-term observations in providing a context for shorter-term studies and allowing analysis of plant community responses to climate variation and disturbance, particularly in the face of ongoing global change.

Key words: annual grassland; California; gopher disturbance; "insurance" hypothesis; long-term experiment; patchiness; rainfall; serpentine; temporal dynamics; weed invasion.

Introduction

The manner in which plant communities change through time and space has been a central concern of ecology, and the need to understand the patterns and processes in vegetation has, if anything, increased in the face of ongoing and increasingly rapid environmental change. Projections of changing climate and incidence of climatic extremes in particular pose important questions in relation to likely ecosystem response (Easterling et al. 2000, Klein Tank et al. 2002, Greenland et al. 2003, Weltzin and McPherson 2003), especially when coupled with changes in land use and disturbance regimes (Chapin et al. 2001).

Davis et al. (2005) recently suggested that contemporary ecology tends to consider vegetation change in a series of largely separate endeavors (for instance, succession ecology, invasion biology, gap/patch dynamics, and global change effects on plant communities) that focus on different causes of vegetation change, e.g., species introduced from other regions of the world, disturbances that create gaps and initiate succession, and global change. In reality, all these influences are likely to be important to a greater or lesser extent and will interact within any particular plant community (Shaw et al. 2002, Zavaleta et al. 2003*a*, *b*), and an understanding of these influences and interactions is essential if we are to understand, manage, and restore ecosystems more effectively in the future.

In this paper, we describe the results of a long-term experimental study in serpentine grassland in the San Francisco Bay Area, California, USA, in which distur-

Manuscript received 11 September 2006; revised 9 March 2007; accepted 21 March 2007. Corresponding Editor: R. W. Ruess.

[3] E-mail: r.hobbs@murdoch.edu.au

bance, climate variation, and introduced species are all important features. Because of its dominance by annual species, small stature, and rapid dynamics, the serpentine grassland system has been viewed as an ideal vehicle for detailed studies of global change processes, nutrient dynamics, and the ecosystem function of biodiversity (e.g., Huenneke et al. 1990, Valentini et al. 1995, Hooper 1998, Dukes and Hungate 2002). The serpentine grassland is also of conservation importance as a refuge for native plant species and as habitat for the listed bay checkerspot butterfly (*Euphydryas editha bayensis*; Ehrlich and Murphy 1987, Murphy and Weiss 1988). Previous studies have highlighted the dynamic nature of the grassland in relation to climatic factors, particularly rainfall, and the importance of small-scale disturbances caused by the activities of pocket gophers (*Thomomys bottae*; Hobbs and Mooney 1985, 1991, 1995).

Here, we present a 20-year data set from experimental plots set up in 1983 with which we explore the following set of questions:

1) How does grassland composition vary in relation to amount and distribution of rainfall?

2) What are the characteristics of the disturbance regime caused by the activities of pocket gophers, and how does this disturbance affect grassland composition and dynamics?

3) What is the additional impact of aboveground grazing on the grassland ecosystem?

4) How do individual grassland species respond to rainfall variation and disturbance, and how does this affect grassland composition through time?

5) Is the invasion of serpentine grassland by nonnative invasive grasses affected by rainfall variation and disturbance?

6) What are the implications of the answers to the above questions in relation to our understanding of ecosystem dynamics and function, species redundancy, invasion biology, and other related topics?

7) In particular, is there evidence to support the "insurance hypothesis" (Yachi and Loreau 1999, Loreau et al. 2002*a*)? This proposes that biodiversity buffers ecosystem processes against environmental changes because different species (or phenotypes) respond differently to these changes, leading to functional compensations among species and hence more predictable aggregate community or ecosystem responses.

METHODS

Study site

The study took place between 1983 and 2002 on Jasper Ridge Biological Preserve in San Mateo County, northern California, USA (122°12′ W, 36°25′ N). The reserve comprises a low-lying ridge (maximum elevation 189 m) on the eastern side of the Santa Cruz Mountains. The study area lies on a serpentine outcrop that bisects the ridge. The soil is characteristically shallow (<40 cm deep), overlying a substrate of ultramafic serpentinite, and is extremely low in nutrients and high in Ni, Mn, and other heavy metals, with a low Ca:Mg ratio (Streit et al. 1993). The area experiences a Mediterranean climate with predominantly winter rainfall and semiarid summers; more than 80% of the year's precipitation falls between November and March, and there is a virtually rain-free period from May to September. Mean annual rainfall over the 35-year period of 1967–2002 is 658 mm, varying greatly among years, from 207 to 1334 mm (Jasper Ridge Biological Preserve, *unpublished data*). The vegetation on the serpentine and adjacent non-serpentine soils has been described by McNaughton (1968) and studied in detail by Hobbs and Mooney (1985, 1991, 1995) and Hobbs and Hobbs (1987). The serpentine grassland is dominated by native annual forbs, but native bunch grasses and geophytes are also typically present. The area was open to grazing by cattle until 1960, but since then has been only subject to grazing by rabbits (*Sylvilagus* spp. and *Lepus californicus*), black-tailed deer (*Odocoileus hemionus*), and pocket gophers (*Thomomys bottae*).

Experimental plots

In November 1982 we established experimental plots on a north-facing slope on the largest area of serpentine on Jasper Ridge. These consisted of control plots, gopher exclosures, and aboveground herbivore (mainly rabbit) exclosures. Three replicated sets of these treatments were established in a randomized block design. The experimental plots are described fully in Hobbs and Mooney (1991). Each plot was 4 × 4 m, and each set of replicates was separated by ~5 m. Within each plot we marked two parallel 1 × 3 m grids, each consisting of 12 contiguous 50 × 50 cm quadrats, giving 24 quadrats per replicate. Each quadrat was subdivided into four 25 × 25 cm subquadrats. Control areas were unfenced, gopher exclosures were fenced with 1-cm mesh fencing buried in the soil to the depth of the bedrock with an aboveground portion of 30–40 cm, and aboveground exclosures were constructed from 1 m high wire mesh (2 cm). The gopher exclosures were only partially successful with all plots being invaded at some time throughout the 20-year study; re-fencing was carried out twice during the 20 years studied. It was concluded that gophers were gaining access to experimental plots not only by breaching fences but also through tunnels in bedrock fissures and that complete exclosures were impossible. Gopher removal from exclosures by trapping was attempted but reinvasion of the plot by more animals was rapid and hence trapping was abandoned. Hence the exclosure treatments are best viewed as reducing the frequency of gopher disturbance rather than completely excluding it.

Rainfall

We analyzed daily precipitation records for Jasper Ridge to document the rainfall regime for the study period. Particularly in the early years of the study some missing data occurred in the Jasper Ridge records. When missing values were encountered we substituted precipitation data from the Woodside Fire Station (National Weather Service), located 3 km to the northwest at 101 m elevation. Rainfall data are presented by growing season (i.e., from September to May) rather than calendar year.

Gopher activity

The presence of new gopher mounds was mapped by a single observer in early April of each year from 1983 to 2002 in the 25 × 25 cm subquadrats in each plot. Gopher activity in each quadrat was assessed as the number of subquadrats with new gopher disturbance, ranging from 0 to 4. Soil depth was also measured in each quadrat, by pushing a graduated metal soil probe into the center of each subquadrat, giving four readings per quadrat.

Plant cover

The percentage of the area of the quadrat covered by each species present was estimated by a single observer (using a subdivided quadrat) in early April of each year. Species nomenclature early in the study followed Munz and Keck (1968) but later changed to Hickman (1993). All plants were identified to species, except for *Brodiaea* spp., which flowered later than the April recording period and could not be reliably differentiated using early-season vegetative characteristics. For some analyses, species were also grouped into six broad life-forms: annual forbs, annual grasses, perennial forbs, perennial grasses, legumes, and geophytes.

Statistical analysis

In the first instance, for all data sets, we used descriptive statistics to analyze the data, and we present summary statistics including mean values and frequency distributions for many of the parameters. We also used randomized block ANOVA to test for differences among treatments for disturbance parameters, functional group cover, and abundance and frequency for selected species in each year and repeated-measures ANOVA to test for year and treatment effects on species numbers (using SPSS 15.0, SPSS, Chicago, Illinois, USA). In order to test the relative variance in species, life-form, and the overall plant community over the course of the study, we used the methods presented by Bai et al. (2004) and computed coefficients of variation in cover (as a percentage) for each organizational level, for both all quadrats combined and by treatment. From these we compared CVs across the different organizational levels to assess the importance of species complementarity and whether there is evidence of the "insurance effect." Rarer species that occurred only sporadically in the data set and had a mean cover near 0% were omitted from the analysis because of instability in CV that arises with means close to zero.

To study community pattern we examined changes in species abundance using nonparametric multivariate analyses in the Plymouth Routines in Multivariate Ecological Research package (PRIMER version 5.2; Clarke and Gorley 2001) described by Clarke and Warwick (2001). An association matrix using Bray-Curtis similarity was calculated for the ordinations; no data standardization was carried out. We subjected the data to a series of transformations (no transformation, square-root, fourth root, and presence/absence) to determine the degree to which the less abundant species contributed to the observed community patterns (Clarke and Gorley 2001, Clarke and Warwick 2001). No transformation resulted in the analysis being strongly influenced by the more abundant species, with the transformations progressively de-emphasizing the common species and presence/absence giving every species equal weight. We used analysis of similarities (ANOSIM) in the PRIMER package to determine whether statistically significant assemblage differences existed between selected sample groups. If two groups of sampling units are really different in their species composition, then compositional dissimilarities between the groups ought to be greater than those within the groups. The ANOSIM statistic R is based on the difference of mean ranks between groups and within groups. The statistical significance of observed R is assessed by permuting the grouping vector to obtain the empirical distribution of R under the null model (Clarke and Gorley 2001). The species responsible for the observed differences were then identified for some data sets using the similarity percentages (SIMPER) procedure in the PRIMER package. Rainfall was superimposed onto some of the ordinations to examine the relationship between the biotic clusters and climatic parameters. We further explored the relationship between species abundance and rainfall and species abundance and disturbance by constructing correlation matrices using Spearman rank order correlations (Statistica version 6; Statsoft, Tulsa, Oklahoma, USA).

Further analysis was carried out on the effect of frequency of gopher disturbance on species composition, using percent cover data from 2002. Quadrats were selected (from any of the treatments) that had been disturbed in two, four, or eight years of the 20-year study period. Two sets of data were analyzed, including and excluding the rabbit exclosure treatment. Data were subjected to nonparametric multidimensional scaling, ANOSIM, SIMPER and Spearman rank order correlations as above.

RESULTS

Rainfall variation

Rainfall data from the Jasper Ridge Biological Preserve records illustrates the variation in annual (July to June), autumn, and winter rainfall experienced during the study (Fig. 1a). This region of the world is influenced by the El Niño Southern Oscillation, and this is reflected

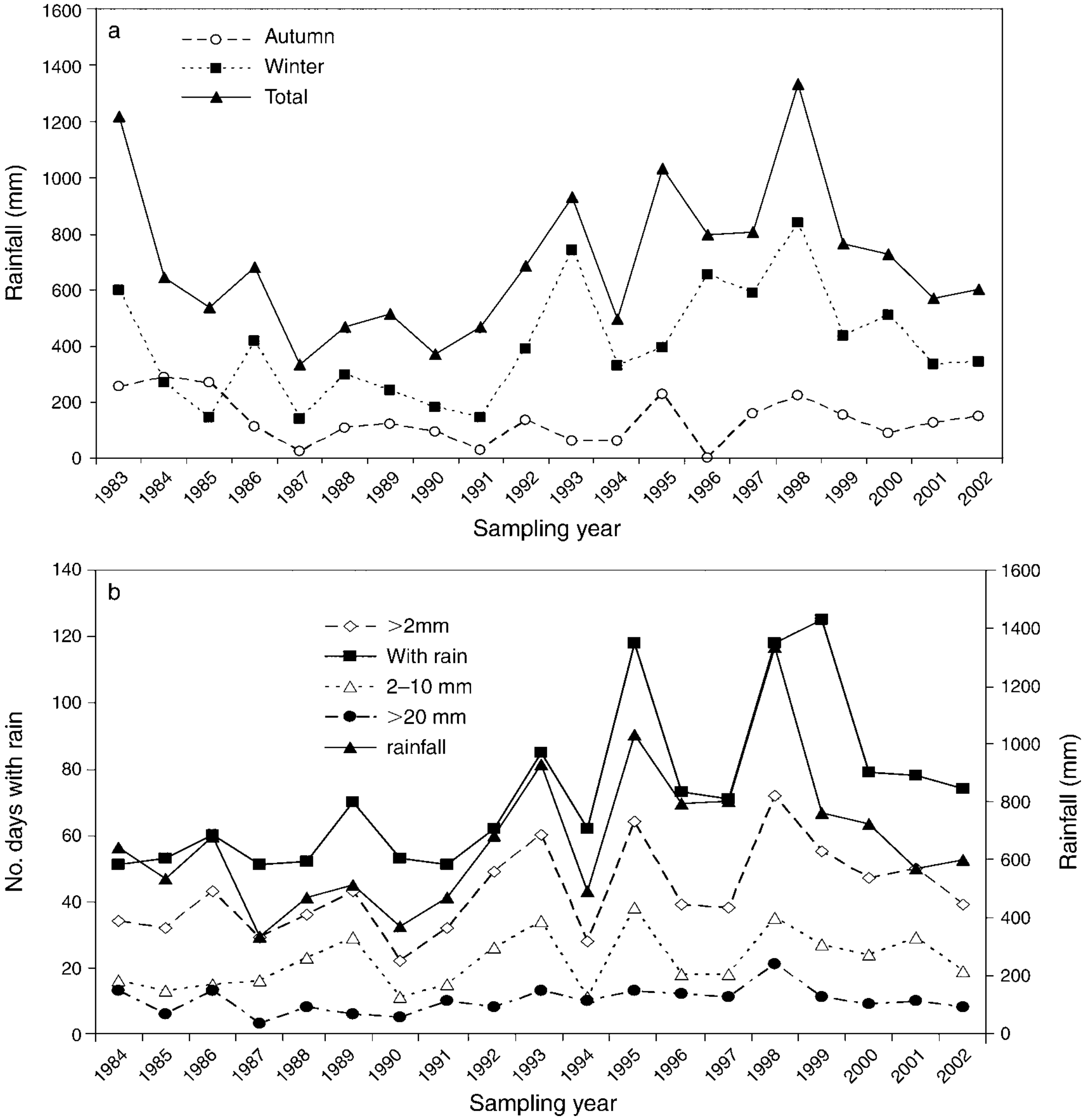

FIG. 1. Rainfall at Jasper Ridge, California, USA, over the period 1983–2002. (a) Annual rainfall (measured from July through June), autumn rainfall (September through November), and winter rainfall (December through February). (b) The number of days with rain during the September–May period and number of days experiencing >2, 2–10, and >20 mm rain; total rainfall is also indicated (1983 data were not available).

by the fourfold difference in total rainfall throughout the 20-year study period. Annual rainfall ranged from 334 mm in 1986–1987 to 1334 mm in 1997–1998, with a 20-year average of 698 mm. The study commenced in the 1982–1983 season with a strong El Niño event and corresponding high rainfall (1214 mm), but rainfall declined in subsequent years, resulting in a period of sustained drought from the 1986–1987 season to the 1990–1991 season. The average rainfall for that five-year period was ~430 mm. Rainfall increased after this with the 1992–1993, 1994–1995, and 1997–1998 seasons having particularly high annual rainfall amounts. Seasonal rainfall also varied greatly throughout the 20 years with autumn rainfall ranging from 1 mm (1995–1996) to 276 mm (1983–1984) and winter rainfall ranging from 141 mm (1986–1987) to 835 mm (1997–1998). Note that high or low autumn or winter rainfall did not in all cases correspond with high or low total rainfall; in particular autumn rainfall did not always reflect the annual rainfall and was less variable than winter rainfall.

The timing of rainfall may be ecologically very important, and so we analyzed the cumulative monthly rainfall for each growing season up to and including the month of the census (April). The timing and the amount of rainfall is highly variable from year to year, with some potential growing seasons starting early in autumn and others starting considerably later (Table 1a). In some years, small amounts of rainfall were recorded in August. September rainfall throughout the 20 years ranged from 0 to 25 mm, by October the rainfall experienced for the season ranged from 0 to 94 mm, and by November it ranged from 1 to 276 mm. It should be noted that no generalizations can be made about the timing of rain and the final amount of rain. A late start to the season did not necessarily coincide with low overall rainfall; for example 1995–1996 was one of the wettest in the study period despite having the latest onset of rain. Similarly, low rainfall did not always coincide with a short growing season (for example 1989–1990), and an early start to the season did not in all cases coincide with high rainfall. For example 1986–1987 had the highest September rainfall but was one of the driest years throughout the entire 20 years. Therefore, it is clear that in addition to the amount of cumulative rainfall varying throughout the season, the proportion of the seasonal rainfall this represents also varies greatly. In 1984–1985, 55% of the season's rain had been recorded by the end of autumn. In contrast, in 1995–1996 none had been recorded by this time (Table 1b). By the end of December accumulated rainfall ranged from 14% to 82% of the period's total, and even by the end of February (the end of winter) an enormous range existed in the proportion of rainfall so far received (34–94%). This is important in terms of absolute rainfall received, which is what plants are most likely responding to. For example, there is a sevenfold variation in absolute rainfall by the end of December (probably most relevant to germination), sixfold by the end of February, and fourfold by the end of March (the main growing period for early-season plants).

In addition to the amount of rain and its distribution, we also analyzed the frequency of rainfall from the beginning of autumn through to April. Fig. 1b shows the total number of days with recorded rain; because many of the days experienced very little rain we also present data for the number of days with >2 mm rain. The number of days with >2 mm rain ranges from 22 in 1990 to 72 in 1998. Comparing Fig. 1a and 1b, the close relationship between the number of days with rain and the total rainfall is evident. Not only do the wet years in the study period have more days with rain but they also have higher rainfall per day (since the number of days with >10 mm and >20 mm also follow the same trends; Fig. 1b). By the end of autumn the number of wet days that occurred ranged from 0 (1995–1996) to 17 (1984–1985) and by the end of winter ranged from 14 (1990–1991) to 54 (1997–1998).

Patterns of gopher disturbance

The gopher disturbance regime was extremely complex and varied both spatially and temporally (Fig. 2). Analysis of the data showed that there was no significant relationship between rainfall amounts and gopher disturbance. In the plots continuously open to gopher activity (control and rabbit exclosure) marked variations are apparent not only from year to year but also from plot to plot in the same year. During the 20-year period the percentage of subquadrats disturbed within a plot ranged from 0 to 86% and between plots in the same year, for example 1990, ranged from 0 to 73% (Fig. 3). All gopher exclosures modified the disturbance regime by reducing the amount of disturbance but complete exclusion of gophers was successful for limited periods only throughout the 20 years (Fig. 3). Little or no gopher disturbance occurred within the exclosures in the first two years of the study. Thereafter, gopher replicate 1 was free of gopher activity from 1987 to 1993 and again from 1995 to 2001, replicate 2 was activity-free only and from 1992 to 1995, and replicate 3 was disturbance-free from 1988 to 1992 and from 1996 to 2000. The greatest level of gopher activity occurred in the aboveground herbivore (rabbit) exclosures (Fig. 3). The mean number of subquadrats disturbed per replicate per year over the 20 years of the study was 20.0 ± 1.0 (mean ± SE) in the control plots, 13.4 ± 1.6 in the gopher exclosure plots, and 30.1 ± 3.6 in the rabbit exclosure plots. Despite notable variation among replicates, particularly in the rabbit exclosures, the treatment means were significantly different, as tested by randomized block ANOVA, at $P < 0.05$.

The extent and frequency of disturbance was assessed over time in quadrats (rather than subquadrats) as this was the level used for vegetation analysis. Analysis of the number of times a quadrat was disturbed over the 20-year period provided data on frequency of disturbance, and this is presented in Fig. 4. In the 20 years of the study, in all treatments, no quadrats remained undisturbed; in the control plots the number of years a quadrat was disturbed ranged from 2 to 12, in rabbit exclosure plots the range was from 2 to 17, and in the gopher exclosures the range was from 1 to 8. The greatest frequency of disturbance occurred in quadrats from which rabbits were excluded; the number of years a quadrat was disturbed in control plots (all three replicates combined) was 6.2 ± 0.3 yr, in gopher exclosure plots was 3.9 ± 0.2 yr, and where rabbits were excluded was 8.7 ± 0.3 yr. These treatment means were significantly different at $P < 0.01$, as tested by randomized block ANOVA.

The extent of disturbance per quadrat could range from zero subquadrats disturbed to four subquadrats disturbed. The number of years with zero disturbance in quadrats was highest in gopher exclosure plots (16.1 ± 0.2 yr) and lowest in the rabbit exclosures (11.3 ± 0.3 yr); the reverse is true for the number of years with quadrats with all four subquadrats disturbed, which was highest in rabbit plots (3.7 ± 0.3 yr) and lowest in gopher plots (1.6 ± 0.1 yr). To summarize, the lowest frequency of disturbance and extent of disturbance occurred in the gopher-excluded plots and the greatest

TABLE 1. Rainfall at Jasper Ridge, California, USA, over the period 1982–2002 shown as (a) total cumulative rainfall in each month between September and April and (b) cumulative monthly rainfall between September and April, expressed as a percentage of the total growing season rainfall.

Month	1982–1983	1983–1984	1984–1985	1985–1986	1986–1987	1987–1988	1988–1989	1989–1990	1990–1991	1991–1992
a) Cumulative monthly rainfall totals (mm)										
Autumn										
Sep	25	6	0	3	25	1	1	13	5	0
Oct	93	9	83	28	25	38	6	63	13	86
Nov	257	276	262	110	26	102	113	102	28	130
Winter										
Dec	379	482	308	192	67	252	197	104	92	228
Jan	612	497	327	275	152	383	247	194	100	302
Feb	852	554	382	527	293	394	287	282	171	522
Spring										
Mar	1090	587	475	671	330	394	423	309	491	651
Apr	1198	591	475	678	334	448	449	317	500	667
b) Cumulative percentage monthly rainfall										
Autumn										
Sep	2	1	0	0	7	0	0	4	1	0
Oct	8	1	18	4	7	8	1	20	3	13
Nov	23	47	55	16	8	23	25	32	6	19
Winter										
Dec	32	82	65	28	20	56	44	33	18	34
Jan	51	84	69	41	46	85	55	61	20	45
Feb	71	94	80	78	88	88	64	89	34	78
Spring										
Mar	91	99	100	99	99	88	94	98	98	98
Apr	100	100	100	100	100	100	100	100	100	100

frequency and extent of disturbance occurred when rabbits were excluded; control plots were intermediate.

Soil depth varied considerably across the experimental plots, with a range of 2–45 cm and a mean of 18.1 cm (SD = 8.94). The number of times a quadrat was disturbed by gophers was positively correlated with soil depth ($r = 0.297$, $P < 0.01$, $n = 144$) when only the quadrats open to gopher disturbance throughout the study period were considered.

An analysis of the mean number of times 50 × 50 cm quadrats were disturbed in 20 years provides an estimate of the likely return time of disturbance; in plots with gophers excluded the likely return time of disturbance is once every 5.1 yr, in control plots disturbance occurs on average once every 3.2 yr, and when rabbits are excluded the rate of disturbance increases to once every 2.3 yr. The likelihood of disturbance occurring in two consecutive years was lowest when gophers were excluded and highest when rabbits were excluded.

Patterns of species abundance

Plots supported a diverse flora that was dominated by annual species; a total of 36 species was identified within the experimental plots throughout the study period (Table 2). For ease of interpretation and reference to previous studies, both the Munz and Keck (1968) and Hickman (1993) nomenclatures are given in Table 2. Otherwise, species names throughout the paper follow Hickman (1993).

The temporal and spatial distribution of species varied greatly, and not all species were present at all times or in all plots (Table 2). Thirteen species were present for the entire 20-year period in all treatment plots, for example, *Agoseris heterophylla*, *Calycadenia multiglandulosa*, and *Lasthenia californica*, whereas some species occurred in very few years or in differing numbers of years depending upon whether rabbits or gophers were excluded, for example, *Gilia clivorum*, *Melica californica*, and *Plagiobothrys nothofulvus* (Table 2). The most abundant species were the early-season annual forbs *Plantago erecta*, *Lasthenia californica*, *Microseris douglasii*, and the late-season forb *C. multiglandulosa*.

Table 2 also documents the range of abundance over the 20-year period for each species in each treatment. For example, in the control treatment, the mean percent cover of *C. multiglandulosa* ranged from 2.3% to 27% and of *Elymus multisetus* from 2% to 9%. Data on the range of change in spatial distribution (i.e., the maximum and minimum percentage of quadrats in which the species occurs) indicate that in some years some species disappeared from all quadrats but were very frequent in other years (Table 2). For example, in the control plots, *Astragalus gambellianus* was found in only 1.4% of quadrats in one year, but in 59.7% in another, and likewise *Microseris douglasii* almost disappeared in one year (present in 0.2% of quadrats), but occurred in almost 50% of quadrats in other years.

TABLE 1. Extended.

1992–1993	1993–1994	1994–1995	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002
0	1	1	0	0	0	7	7	1	6
51	17	12	0	15	21	34	23	94	19
62	59	228	1	158	223	155	89	122	146
310	155	296	205	444	319	193	98	147	377
630	224	606	456	733	662	369	319	270	428
797	388	618	654	748	1058	588	598	454	489
858	395	905	719	761	1156	686	654	513	566
880	457	963	754	785	1230	755	695	563	579
0	0	0	0	0	0	1	1	0	1
6	4	1	0	2	2	5	3	17	3
7	13	24	0	20	18	20	13	22	25
35	34	31	27	57	26	26	14	26	65
72	49	63	60	93	54	49	46	48	74
91	85	64	87	95	86	78	86	81	84
97	87	94	95	97	94	91	94	91	98
100	100	100	100	100	100	100	100	100	100

These patterns are discussed in more detail later for selected species.

Data on the average abundance of the six life-forms present in the quadrats (Fig. 5) indicate that the most dramatic variation throughout the study period occurs in the annual grasses whereby they virtually disappear from 1988 to 1992; during that period geophyte abundance increased markedly and other groups had a more consistent abundance. The trends in treatment effects can also be observed in Fig. 5, whereby reduced rabbit grazing reduced abundance of perennial grasses (mean cover was significantly lower over the 20-year period; $P < 0.05$) but showed a trend of increasing legume abundance (mean cover was significantly higher over the 20-year period; $P < 0.05$). Decreased gopher activity resulted in periodically increased geophyte abundance.

An analysis of individual species showed considerable changes in abundance over the 20-year study (Fig. 6).

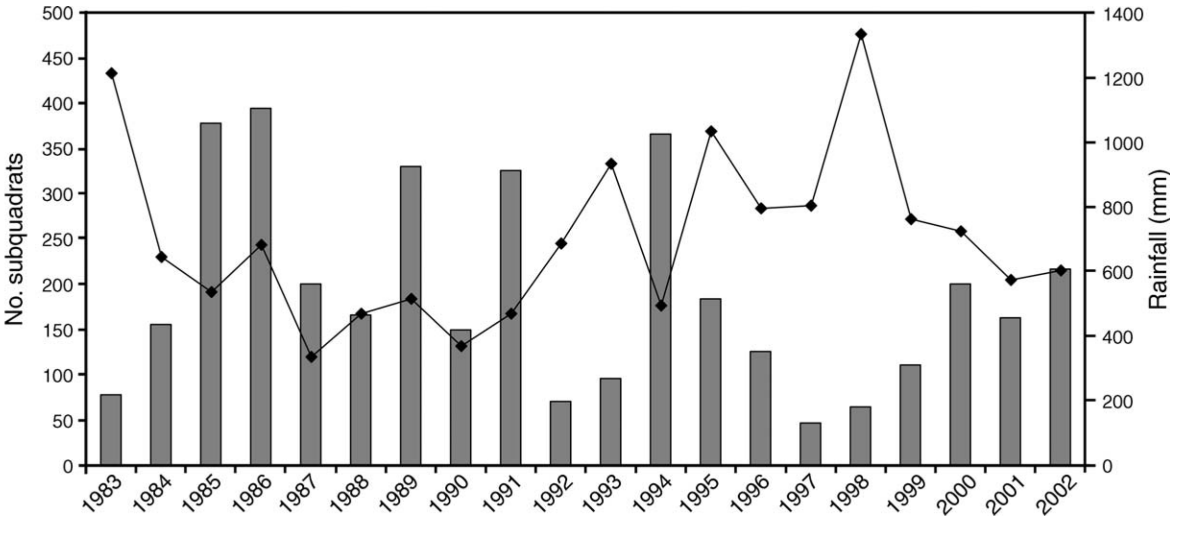

FIG. 2. Total number of 25 × 25 cm subquadrats disturbed by gopher activity across all plots and treatments in each year 1983–2002 (bars and left-hand y-axis), with total annual rainfall also indicated (line and right-hand y-axis).

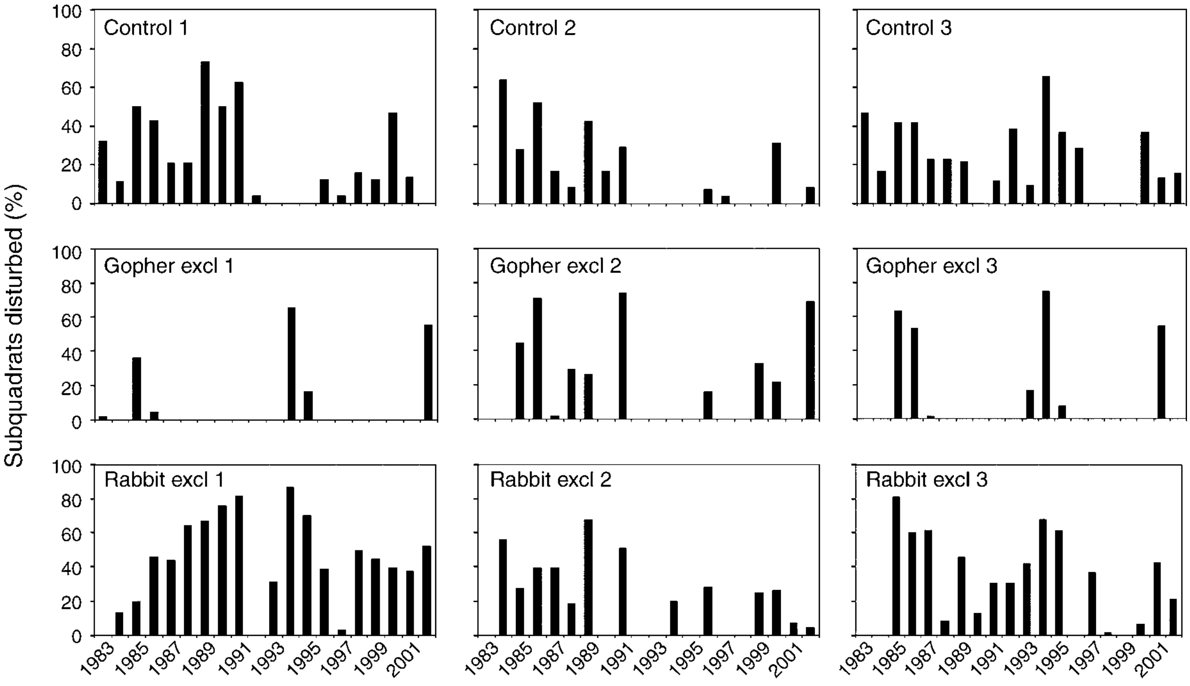

FIG. 3. Percentage of 25 × 25 cm subquadrats (out of a total of 96) disturbed in each treatment replicate (excl, exclosure) in each year over the period 1983–2002.

Some species, for example, *Bromus hordeaceus*, *Hesperevax sparsiflora*, and *Vulpia microstachys* var. *microstachys*, have no or very low abundance during the sustained low rainfall period and increased in abundance as rainfall increased, whereas *Brodiaea* sp. and *M. douglasii* increased in abundance during periods of low rainfall and decreased as annual rainfall began to increase. The interaction between dominant species is

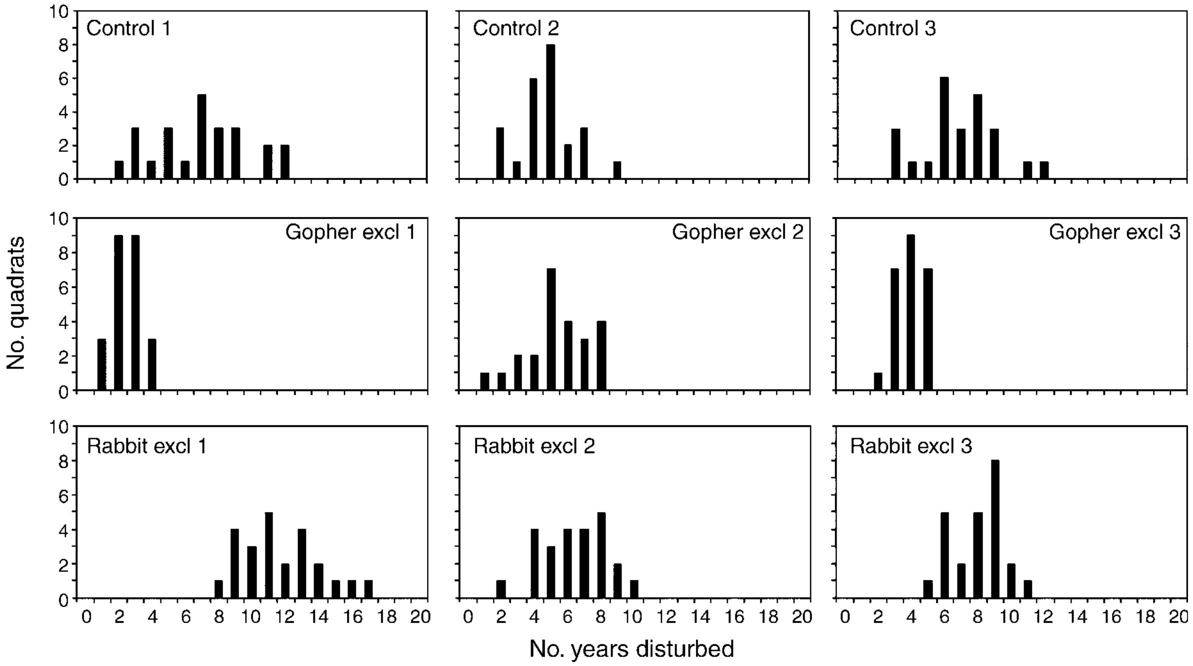

FIG. 4. Number of quadrats experiencing gopher disturbance multiple times over the 20 years between 1983 and 2002, in each treatment replicate (excl, exclosure). The panels show the number of years any given quadrat was disturbed and the number of quadrats experiencing that number of disturbances.

also interesting; for example, *P. erecta* and *M. douglasii* responded in opposite ways to the sustained drought conditions in the middle of the study. Correlations between the abundance of the 36 species and rainfall amounts (autumn, winter, or total) were significant ($n = 72$ quadrats, $P < 0.05$) for 18 of the species in at least one treatment (Table 3). All of the perennial grasses and geophytes showed a significant correlation with rainfall as did four of the five annual grasses. Only 5 of the 18 annual forbs showed a significant correlation with rainfall; winter rainfall influenced more species than autumn rainfall. We also analyzed for potential lag effects of rainfall by correlating abundances of selected species against the previous year's rainfall total, the sum of the current and previous year's total rainfall, and the sum of the current and previous two years' total rainfall. While correlation coefficients were increased in some cases, no further significant results over and above those indicated in Table 3 were found.

The influence of excluding gophers and rabbits varied among species (Fig. 6). Some species, such as *P. erecta*, *C. multiglandulosa*, and *H. sparsiflora*, showed little treatment effect with treatments tracking one another very closely over time. By contrast, *Hemizonia congesta* subsp. *luzulaefolia* abundance increased when rabbits and gophers were excluded, particularly post-drought. The perennial grasses *Elymus multisetus* and *Nassella pulchra* were less abundant in the rabbit exclosures and the legume *Lotus subpinnatus* was generally more abundant when rabbits were excluded. In some species the exclusion of gophers and rabbits led to an increased sensitivity to rainfall variation whereby a significant correlation with rainfall occurs in the exclosures but not in the control plots, for example, *A. gambellianus* and *Brodiaea* spp. (Table 3).

Another measure of the occurrence of species in the study plots is the frequency with which they were encountered, that is, the percentage of quadrats within which the species occurred in each year (Fig. 7). Comparing Figs. 6 and 7 we see that abundance and the frequency of distribution response varied greatly between species over the 20-year study (see also Table 2 for maximum–minimum ranges). For example, in *P. erecta* abundance changed markedly with time but it was still present in almost all quadrats under all rainfall regimes and all treatments. By contrast, the spatial distribution of *E. multisetus* mirrored abundance. Other species responded in a manner somewhat between these two extremes; for example, *Brodiaea* spp. distribution varied to a lesser extent than its abundance and *C. multiglandulosa* had periods of reduced frequency that were partially mirrored by changes in abundance.

Clearly, not only are changes in abundance and spatial distribution over time important, so is the overall extent of that change, as this provides information on the species stability within the community and its ability to maintain its abundance and presence under different conditions. In all species presented, abundance is more sensitive to change from year to year than spatial distribution (Table 4); abundance ranges from a threefold difference between minimum value and maximum value (*E. multisetus*) to greater than a thousandfold difference (*B. hordeaceus* and *M. californicus*), whereas spatial distribution ranges from virtually no difference between minimum value and maximum value (*P. erecta*) to a 67-fold difference (*B. hordeaceus*). Just as there was great temporal variation in the response to rainfall, response to the exclusion of rabbits and reduced gopher activity was also highly variable. In some species, for example, *L. californica* and *P. erecta*, exclusion of rabbits and reduced gopher activity had little effect on the range of values. The exclusion of rabbits increased the ratios for *E. multisetus* and *C. pomeridianum* but decreased the ratios for *H. sparsiflora*. Reduced gopher activity increased the ratios for *N. pulchra* and decreased the ratios for *L. platyglossa*.

Patterns of species richness

The mean number of species present per quadrat per year over the 20-year period of the study (Fig. 8) gives an indication of trends in overall community richness. All treatments responded in a similar manner and reflected total rainfall, with lowest species richness occurring from 1988 to 1994, throughout and subsequent to the drought period (approximately seven species per quadrat), and highest species richness occurring in the wettest years of 1983, 1995, and 1998 (11–12 species per quadrat). Repeated-measures ANOVA indicated a significant year effect ($F = 5.83$, df $= 2, 8$, $P < 0.05$) but no significant treatment effect ($F = 5.72$, df $= 2, 4$, NS), although significant differences among treatments were present in some individual years (e.g., in 1984, numbers of species were 11.53 ± 0.23 in the controls, 10.89 ± 0.23 in gopher exclosures, and 9.83 ± 0.17 in the rabbit exclosures). Numbers of species over the 20-year period were 9.94 ± 0.06 in the control plots, 9.93 ± 0.06 in the gopher exclosures, and 9.39 ± 0.06 in the rabbit exclosures.

The total number of species present in each plot (i.e., over all 24 quadrats), ranged from 15 to 22, again varying in relation to rainfall amounts. Repeated-measures ANOVA again indicated a significant year effect ($F = 8.93$, df $= 2, 8$, $P < 0.01$) but no significant treatment effect ($F = 4.38$, df $= 2, 4$, NS). Species numbers over the 20-year period were 20.76 ± 0.07 in control plots, 19.83 ± 0.07 in gopher exclosures, and 20.00 ± 0.08 in rabbit exclosures.

Relative variance in species, life-forms, and community

We carried out analyses for the data as a whole and also on a per treatment basis. However, no obvious differences among treatments were detected, and here we present only the results for the pooled treatments. The coefficients of variation for individual species (calculated on percent cover per quadrat per year over the study period) increased from the most abundant species to the

TABLE 2. Plant species present within 50 × 50 m quadrats (with names as presented in both Munz and Keck [1968] and Hickman [1993] and life-form).

Species name (Jepson manual: Hickman 1993)	Species name (Munz and Keck 1968)	Form	Presence		
			C	G	R
Agoseris heterophylla	*Agoseris heterophylla*	annual forb	20	20	20
Astragalus gambellianus	*Astragalus gambellianus*	legume	20	19	20
Brodiaea sp. + *Triteleia laxa* + *Dichelostemma capitatum*	*Brodiaea* sp. (incl. *B. laxa* and *B. pulchella*)	geophyte	20	20	20
Bromus hordeaceus	*Bromus mollis*	annual grass	20	15	17
Bromus trinii	*Bromus trinii*	annual grass	11	3	8
Calandrinia ciliata	*Calandrinia ciliata*	annual forb	12	7	11
Calycadenia multiglandulosa	*Calycadenia multiglandulosa*	annual forb	20	20	20
Castilleja densiflora	*Orthocarpus densiflorus*	annual forb	20	20	19
Chlorogalum pomeridianum	*Chlorogalum pomeridianum*	geophyte	20	20	20
Crassula connata	*Tillaea erecta*	annual forb	19	13	16
Elymus multisetus	*Sitanion jubatum*	perennial grass	20	20	20
Epilobium brachcarpum	*Epilobium paniculatum*	annual forb	18	17	18
Escholtzia californica	*Escholtzia californica*	perennial forb	18	17	18
Gilia clivorum	*Gilia clivorum*	annual forb	2	3	18
Hemizonia congesta subsp. *luzulaefolia*	*Hemizonia luzulaefolia*	annual forb	20	20	20
Hesperevax sparsiflora	*Evax sparsiflora*	annual forb	20	20	20
Lasthenia californica	*Lasthenia californica*	annual forb	20	20	20
Layia platyglossa	*Layia platyglossa*	annual forb	20	20	16
Lepidium nitidum	*Lepidium nitidum*	annual forb	7	4	14
Linanthus androsaceus	*Linanthus androsaceus*	annual forb	1	1	0
Lolium multiflorum	*Lolium multiflorum*	annual grass	6	2	7
Lomatium utriculatum	*Lomatium utriculatum*	perennial forb	1	11	8
Lotus subpinnatus	*Lotus subpinnatus*	legume	20	20	20
Melica californica	*Melica californica*	perennial grass	1	1	10
Micropus californicus	*Micropus californicus*	annual forb	19	20	20
Microseris douglasii	*Microseris douglasii*	annual forb	20	20	20
Minuartia douglasii	*Arenaria douglasii*	annual forb	1	0	0
Nassella pulchra	*Stipa pulchra*	perennial grass	20	20	14
Plagiobothrys nothofulvus	*Plagiobothrys nothofulvus*	annual forb	2	18	10
Plantago erecta	*Plantago erecta*	annual forb	20	20	20
Poa secunda subsp. *secunda*	*Poa scabrella*	perennial grass	20	20	20
Trifolium albopurpureum	*Trifolium albopurpureum*	legume	6	7	7
Trifolium sp.	*Trifolium* sp.	legume	9	11	7
Trifolium tridentatum	*Trifolium tridentatum*	legume	1	3	3
Vulpia microstachys var. *microstachys*	*Vulpia microstachys* var. *microstachys*	annual grass	20	20	20

Notes: Presence is expressed as the number of years (out of 20) that a species was present within replicate plots in control (C), gopher exclosures (G), and rabbit exclosures (R). Cover is expressed as the maximum and minimum mean percent cover within 50 × 50 cm quadrats over the 20-year period between 1983 and 2003 in control plots, gopher exclosures, and rabbit exclosures. Frequency is expressed as the maximum and minimum percentage of quadrats the species occupied over the period 1983–2002 in control plots, gopher exclosures, and rabbit exclosures.

rarer species (Fig. 9a). For life-form groups, the coefficient of variation was very low for annual forbs, the most abundant group, and very high for perennial forbs, the least abundant group (Fig. 9b). Otherwise, the relative size of the CV did not follow the relative ranking of the groups. In particular, annual grasses, ranked second in terms of cover, had the third highest CV. The mean CV for species was significantly higher than that for life-form, which was in turn higher than for the plant community overall (Fig. 9c).

Community pattern

Ordination of the data set revealed both temporal trends and treatment effects on the community pattern. Visual interpretation of the ordination series indicates that dominant species largely influenced the change in composition over time (with varying rainfall regimes) but the intermediate and rare species, although sensitive to rainfall, have more influence on the change in composition in response to treatments (Fig. 10a–d), reflecting previously presented data; this is discussed in more detail below. Ordination results in two and three dimensions were compared. While the stress value was lower for three-dimensional plots, because of the visual complexity, we have chosen to present only the two-dimensional solutions. Results from different transformations of the data are presented.

Using untransformed data (Fig. 10a), where the effect of common species on similarity among samples is emphasized, treatments track one another quite closely over time (see circled years). This remained the case in the three-axis representation of the ordination (not presented here). For control plots, 1983–1986 (years 1–4) are close in ordination space, 1987 (year 5) starts to

Table 2. Extended.

Cover (%)						Frequency (% quadrats)					
C		G		R		C		G		R	
Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
0.1	1.5	0.2	10.2	0.5	5.3	6.9	61.1	18.1	95.8	26.4	94.4
0.1	1.3	0	1.0	0.1	1.5	1.4	59.7	0	47.2	6.9	51.4
0.7	5.1	0.9	10.0	0.9	3.6	41.7	98.6	61.1	100.0	55.6	95.8
0.1	17.2	0	4.1	0	6.8	1.4	94.4	0	88.9	0	83.3
0	0.2	0	0.2	0	6.4	0	12.5	0	2.8	0	19.4
0	0.5	0	0.2	0	5.4	0	11.1	0	4.2	0	29.2
2.3	27.0	2.1	30.9	2.8	28.0	48.6	100.0	50.0	98.6	52.8	97.2
0.1	4.4	0.1	6.4	0	4.7	4.2	95.8	2.8	94.4	0	88.9
0.5	5.2	0.4	4.8	0.2	5.1	12.5	79.2	8.3	81.9	4.2	69.4
0	1.5	0	0.4	0	0.7	0	55.6	0	11.1	0	19.4
2.0	9.0	2.2	7.6	0.1	4.4	33.3	83.8	36.1	61.1	4.2	54.2
0	0.7	0	0.7	0	2.7	0	48.6	0	50.0	0	88.9
0	1.1	0	1.0	0	1.3	0	27.8	0	19.4	0	31.9
0	0.1	0	0.1	0	1.3	0	1.4	0	2.8	0	29.2
0.1	0.6	0.1	8.1	0.1	8.5	1.4	18.1	9.7	79.2	9.7	56.9
0.2	6.7	0.1	5.2	0.2	5.1	6.9	83.3	8.3	87.5	8.3	63.9
2.5	32.2	4.5	48.3	4.0	43.8	63.9	100.0	70.1	100.0	58.3	100.0
0.1	0.9	0.1	1.1	0	1.0	1.4	38.9	4.2	48.6	0	40.3
0	0.1	0	0.1	0	0.6	0	2.8	0	1.4	0	13.9
0	0.1	0	0.1	0	0	0	2.8	0	1.4	0	0
0	0.6	0	0.8	0	0.1	0	4.2	0	6.9	0	2.8
0	0.2	0	0.8	0	0.6	0	4.2	0	12.5	0	9.7
0.6	4.9	0.3	6.9	0.7	15.9	38.9	87.5	25.0	94.4	43.1	100.0
0	0.3	0	0.1	0	0.4	0	5.6	0	2.8	0	4.2
0	2.1	0.1	1.3	0.1	1.2	0	40.3	2.8	27.8	2.8	26.4
0.2	45.8	0.3	27.6	0.8	25.2	8.3	100.0	12.5	100.0	20.8	100.0
0	0.07	0	0	0	0	0	2.8	0	0	0	0
0.2	5.2	0.1	3.9	0	0.4	5.6	41.7	1.4	27.8	0	2.8
0	0.1	0	0.3	0	0.5	0	2.8	0	8.3	0	12.5
9.4	56.1	7.4	51.5	5.6	44.9	97.2	100.0	93.1	100.0	90.3	100.0
0.3	2.1	0.1	2.0	0.1	1.9	5.6	41.7	6.9	52.8	2.8	40.3
0	0.3	0	1.5	0	0.4	0	13.9	0	13.9	0	4.2
0	0.3	0	0.4	0	0.1	0	16.7	0	13.9	0	4.2
0	0.1	0	0.1	0	0.1	0	2.8	0	4.2	0	2.8
0.2	10.0	0.2	23.1	0.2	17.3	11.1	98.6	13.9	97.2	9.7	98.6

drift away, and then there is a large shift in 1988–1990 (years 6–8), followed by further large shifts in 1991 (year 9) and 1992–1995 (years 10–13). In 1996 (year 14) the location starts to move closer to the earlier positions, with further movement back in 1997–1999 (years 15–17) and 2000–2002 (years 18–20) located closest to the initial ordination position. The years showing greatest difference from the start and from one another are 1988 (year 6), 1991 (year 9), and 1993 (year 11). These years represent the early stage of drought, the late stage of drought, and the period after a return to two years of above-average rainfall, respectively (Fig. 1a). Gopher and rabbit exclosure data show roughly similar trends.

Fourth-root transformed data (Fig. 10b) takes some account of rarer species, mixing contributions from both common and rare species, and hence lessens the impact of the dominant taxa on the analysis. In this analysis, the three treatments initially occur in a similar position in ordination space (year 1), but do not track one another over time. For control plots, a similar pattern to that discussed for the untransformed data is apparent. The gopher exclosures show a similar pattern to the control up to 1993 (year 11), but the movements between years are more exaggerated and the points are in some years quite displaced from the other treatments (changing towards the bottom right in the figure). Similarly, the rabbit exclosure points show large differences after 1983 (year 1) and are completely displaced from the other points from 1986 (year 4) onwards (occupying the ordination space in the top and right of the figure).

Using presence/absence data (Fig. 10c) represents the ultimate down-weighting of common species, in that species sufficiently ubiquitous to appear in all samples do not contribute to the final multivariate description. Instead, the emphasis is shifted towards patterns in the intermediate and rarer species and the generally larger numbers of these override the contributions from the few dominant species. The trends evident in the fourth root-transformed data are further enhanced in this ordination, with treatments not tracking one another in ordination space despite similar starting points. In Fig. 10c specific years are circled to highlight the

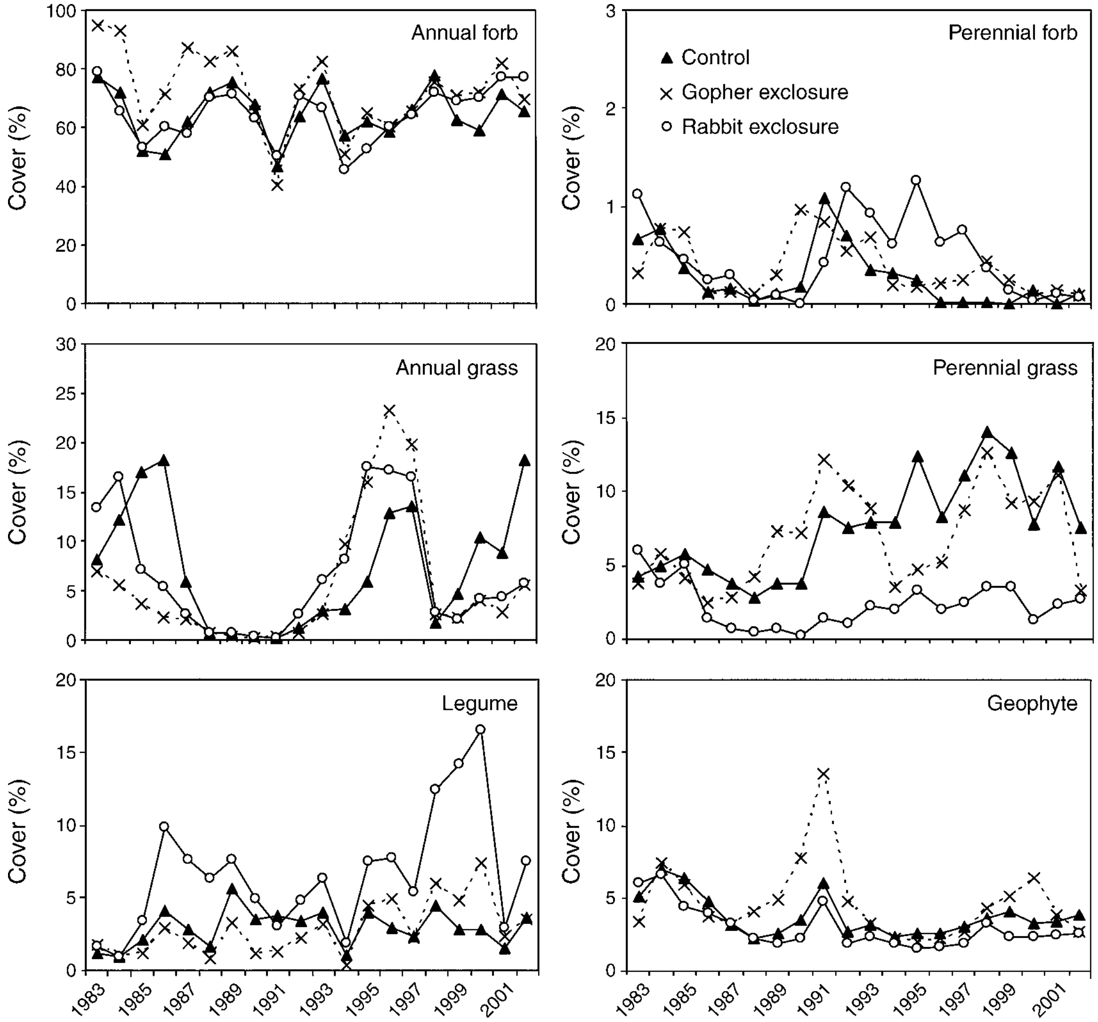

FIG. 5. Mean abundance (percent cover) per quadrat (replicates combined, $n = 72$) for each life-form.

positional differences. The difference between control treatment and gopher exclosure treatment is more pronounced, and a similar relatively large positional difference of the rabbit exclosure treatment is also clear.

Analysis of similarities using treatment (control, gopher exclosures, rabbit exclosures) as a factor and transforming the data in the ways described for ordination showed that reducing the weighting of common species increased the significance of the differences between treatments (untransformed, $R = 0.11$, $P = 0.02$; presence/absence, $R = 0.29$, $P = 0.01$). Analysis of similarities using rainfall categories (<500, 500–700, 701–900, >900 mm total growing season rainfall) as a factor and transforming the data as described showed that reducing the weighting of common species reduced the significant differences between rainfall categories (untransformed, $R = 0.27$, $P = 0.01$; presence/absence, $R = 0.07$, $P = 0.27$). Although significant, the groups were not strongly separated, reflecting the large spread in the data.

This confirms the visual interpretation of the ordinations. The interaction between treatment and rainfall in affecting overall composition is illustrated in Fig. 10d, in which rainfall amounts are superimposed as a bubble plot on the ordination using presence/absence data (shown in Fig. 10c). The largest differences between treatments, particularly between the rabbit exclosures and the other treatments, are found in years with low rainfall amounts.

Effects of disturbance frequency on community composition

Ordination plots of the data from quadrats disturbed in a different number of years during the 20-year study period (i.e., two, four, or eight times) differed depending on whether quadrats from the rabbit exclosures were included or not. Where they were included, there was no clear pattern of separation in 3-D ordination space of the groups with different disturbance regimes. Where only data from the gopher exclosure and control

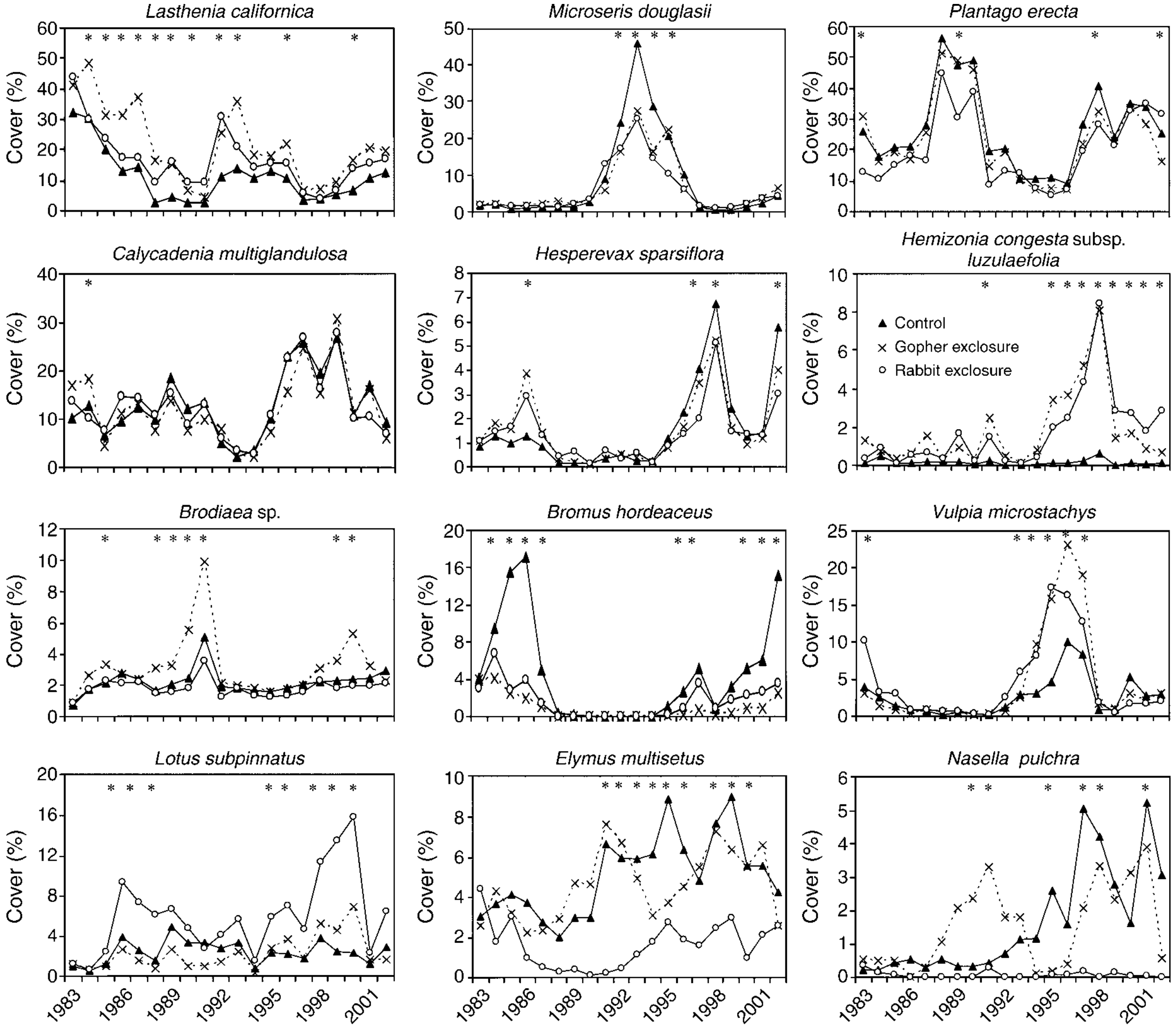

FIG. 6. Mean abundance (percent cover) of selected species within 72 (replicates combined) 50 × 50 cm quadrats in control, gopher exclosure, and rabbit exclosure plots for the period 1983–2002. Asterisks indicate years in which significant differences ($P <$ 0.05 or lower) among treatments were detected, using randomized block ANOVA on annual data.

treatments were used (Fig. 11), there was a clear separation of group 3 (quadrats disturbed in 8 of the 20 years) from groups 1 and 2 (quadrats disturbed in 2 or 4 of the 20 years, respectively).

ANOSIM confirmed the visual representation in the ordination space. Using control and gopher exclosure data ANOSIM showed that group 3 was significantly different from groups 1 and 2 ($R = 0.27$, $P = 0.08$ and $R = 0.29$, $P = 0.01$, respectively), but groups 1 and 2 were not significantly different from one another ($R = 0.04$, $P = 0.76$). That is, quadrats disturbed 8 times in 20 years are different from those disturbed 2 or 4 times in 20 years but quadrats disturbed 2 or 4 years are not different from one another. By comparison, ANOSIM using all quadrats (including those in rabbit exclosures) did not show any significant differences between groups. Group comparisons yielded a global $R = 0.06$, $P = 0.41$.

SIMPER allows the identification of species primarily accounting for the observed assemblage difference, as confirmed to exist by ANOSIM. SIMPER analysis determines the overall percentage of contribution each species makes to the average dissimilarity between two groups and lists in decreasing order of importance the species responsible for discriminating the sets of data. A total of eight species account for 60% of the dissimilarity between group 3 and groups 1 and 2. A positive sign (+) indicates species that were more abundant in group 3 (disturbed eight times), and a negative sign (–) indicates species that were more abundant in groups 1 and 2 (disturbed two or four times): *Agoseris heterophylla* (–), *Bromus hordeaceus* (+), *Calycadenia multiglandulosa* (–), *Hesperevax sparsiflora* (+), *Lasthenia californica* (–), *Microseris douglasii* (+), *Castilleja densiflora* (–), and *Vulpia microstachys* var. *microstachys* (–).

TABLE 3. Spearman rank order correlations between rainfall and mean percentage cover of selected species in 72 quadrats.

	Autumn			Winter			Autumn and winter			Total		
Species	C	G	R	C	G	R	C	G	R	C	G	R
Astragalus gambellianus					+			+			+	+
Brodiaea sp.					–			–			–	
Bromus hordeaceus		+	+									
Bromus trinii						–						
Chlorogalum pomeridianum	+											
Elymus multisetus			+	+					+	+		+
Escholtzia californica		+							+			+
Hesperevax sparsiflora				+			+	+		+	+	
Layia platyglossa				+	+	+	+	+	+	+	+	+
Lepidium nitidum						–			–			
Lolium multiflorum			+									
Lotus subpinnatus					+			+			+	
Melica californica						+			+			+
Nassella pulchra				+								
Plagiobothrys nothofulvus						+			+			+
Poa secunda subsp. *secunda*	+		+					+			+	
Tillaea erecta				+			+		+	+	+	+
Vulpia microstachys var. *microstachys*				+	+	+	+	+	+	+	+	+

Notes: Significant positive (+) or negative (–) correlations at $P < 0.05$ are indicated. Analysis of percent cover data for each species (average of 72 quadrats by year by treatment) was carried out against the following rainfall parameters: autumn rainfall, winter rainfall, autumn plus winter rainfall, and total rainfall. Autumn is defined as the months of September, October, and November; winter is defined as December, January, and February. Key to abbreviations: C, control; G, gopher exclosures; R, rabbit exclosures.

Spearman rank order correlations indicated a significant correlation with number of years disturbed in 20 for *Plantago erecta* (+) and for *Agoseris heterophylla*, *Brodiaea* spp., *Chlorogalum pomeridianum*, *Lasthenia californica*, *Castilleja densiflora*, and *Vulpia microstachys* var. *microstachys* (all –).

Species displaying a significant correlation with years since last disturbance were: *Agoseris heterophylla*, *Calycadenia multiglandulosa*, *Chlorogalum pomeridianum*, *Castilleja densiflora*, and *Hemizonia congesta* var. *luzulaefolia* (positive correlation; i.e., species cover increases as length of time from disturbance increases), and *Bromus hordeaceus*, *Microseris douglasii*, and *Plantago erecta* (negative correlation).

DISCUSSION

Here we revisit the questions posed in the introduction and examine them in the light of the results presented. This study has presented data spanning 20 years and as such sets a valuable longer term context for many of the short-term studies carried out in the serpentine grassland and, we hope, provides important insights into the dynamics of the grassland ecosystem.

Grassland composition in relation to rainfall

The study spanned a period of dramatic variations in annual rainfall amounts and distributions, starting with the very high rainfall years at the commencement of the study that coincided with the strongest El Niño event experienced to that point in California. The impacts of El Niño variations and the climatic extremes that accompany them have been increasingly discussed in the literature (e.g., Hobbs and Mooney 1996, Holmgren et al. 2001, McPhaden et al. 2007). Glantz (2001) has pointed out that the 1997–1998 and 1982–1983 El Niños were the strongest such events during the 20th century. However, the two events did not translate into a similar set of grassland dynamics, probably on account of the different timings of onset of El Niño conditions (the 1997–1998 event developed rapidly in February 1997 and decayed more rapidly than previous events; Glantz 2001). Indeed, no two years in the 20-year study can be said to be completely similar in terms of grassland composition and species abundances. The middle period of the study was characterized by several years of below-average rainfall, and this was reflected in dramatic shifts in the grassland composition and in overall species abundances.

Our results build on those from previous papers. The clear patterns of dominant species response to rainfall amounts reported in Hobbs and Mooney (1991) reflected the fact that the study period (1983–1988) spanned a period of almost monotonically declining rainfall. Hence species response patterns reflected this. However, in Hobbs and Mooney (1995), the study period had expanded to include a more varied rainfall pattern and species responses were not as clear, which was interpreted as being presumably due to hysteresis effects. While some relatively clear responses to rainfall remain obvious in the 20-year data set, some of the clearest responses reported in Hobbs and Mooney (1991) are no longer so simple to detect (for instance, the correlation between total rainfall and abundance of the dominants, *Plantago erecta* and *Lasthenia californica*), again presumably reflecting hysteresis or lag effects (as found, for instance by Adler and Levine [2007]). However, we have not been able to detect these

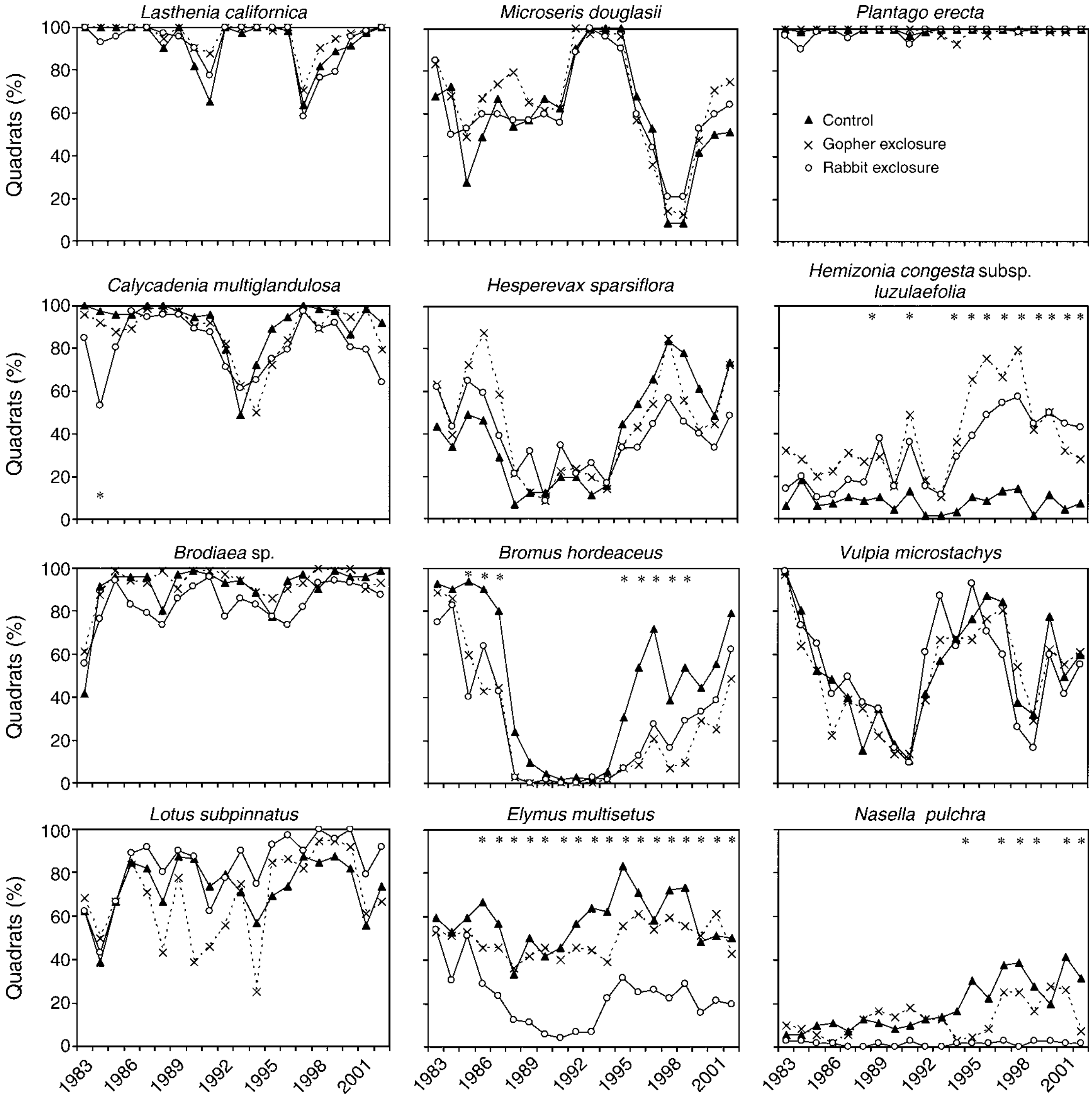

FIG. 7. Mean frequency (percentage of quadrats in which the species occurred) of selected species within 72 (replicates combined) 50 × 50 cm quadrats in control, gopher exclosure, and rabbit exclosure plots for the period 1983–2002. Asterisks indicate years in which significant differences ($P < 0.05$ or lower) among treatments were detected, using randomized block ANOVA on annual data.

using simple correlational analyses comparing species abundances with rainfall amounts in previous years.

Other recent studies have highlighted the likely importance of increased incidence of extreme events such as droughts, as predicted in current climate change scenarios, in affecting grassland community dynamics (Morecroft et al. 2004). Our results, in which species numbers dropped during the extended drought experienced during the study, mirror those of Tilman and El Haddi (1992) except that recovery of diversity was more rapid in our case. In addition Haddad et al. (2002) indicated that single occurrences of disturbances such as drought could have long-term impacts on grassland ecosystems that continued for at least nine years. If similar long-term impacts of episodic events are important in the serpentine grassland, this essentially would mean that the grassland system was simultaneously influenced by several such episodes, given the distribution of high- and low-rainfall periods in the current study. This would then make teasing out the relative effects of different events very difficult.

A more mechanistic analysis may yield more insight; however, we do not consider the mechanisms behind the observed patterns in any detail here. Changing species composition and individual species performance in relation to rainfall have been noted in other systems and explained in differing ways. For instance, Silvertown et al. (1994) concluded that rainfall had an indirect

TABLE 4. Ratio of maximum to minimum for mean percent cover and frequency of occurrence (the percentage of the number of quadrats the species occurs in of the total number of quadrats in the treatment) for selected species, which could only be calculated if the species does not disappear completely in any year.

	Abundance			Frequency		
Species	C	G	R	C	G	R
Agoseris heterophylla	20	43	10	9	5	4
Astragalus gambellianus	65		15	43		7
Brodiaea spp.	7	11	4	2.4	1.6	1.7
Bromus hordeaceus	>1000			67		
Calycadenia multiglandulosa	12	15	10	2.1	2.0	1.8
Chlorogalum pomeridianum	11	13	34	6	10	16
Elymus multisetus	4	3	34	2.5	1.7	13
Hemizonia congesta var. *luzulaefolia*	64	62	85	13	8	6
Hesperevax sparsiflora	45	47	34	12	10	8
Lasthenia californica	13	11	11	1.6	1.4	1.7
Layia platyglossa	89	27		28	12	
Lotus subpinnatus	8	21	23	2.2	3.8	2.3
Micropus californicus		33	>1000		10	9
Microseris douglasii	305	106	31	12	8	5
Nasella pulchra	28	389		7	20	
Plantago erecta	6	7	8	1	1	1
Vulpia microstachys var. *microstachys*	59	122	96	9	7	10

Note: Abbreviations are: C, control; G, gopher exclosures; R, rabbit exclosures.

effect on temperate grassland composition via rainfall effects on overall biomass. In an experimental study in grassland, Suttle et al. (2007) concluded that short-term changes in rainfall had pronounced effects on individual species, but that, as altered rainfall regimes were maintained for a number of years, feedbacks and species interactions overrode individual species responses. Chesson et al. (2004) focused on plant traits that facilitate survival and growth in arid environments and result in differing responses to rainfall pulses. Indeed, the idea of precipitation pulses as drivers of arid/semiarid ecosystems has received increasing attention recently (e.g., Huxman et al. 2004, Schwinning et al. 2004, and other papers in that issue), and it may be useful to consider the dynamics of Mediterranean-climate systems in a similar way (e.g., Scher et al. 2004). Indeed, Goldberg and Novoplansky (1997) highlighted the importance of understanding species responses to pulse and inter-pulse periods in unproductive environments such as the serpentine grassland. We aim to discuss such considerations further in a later paper.

Disturbance regime and grassland composition and dynamics

Gophers represent a prime example of an ecosystem engineer (Jones et al. 1997, Reichman and Seabloom

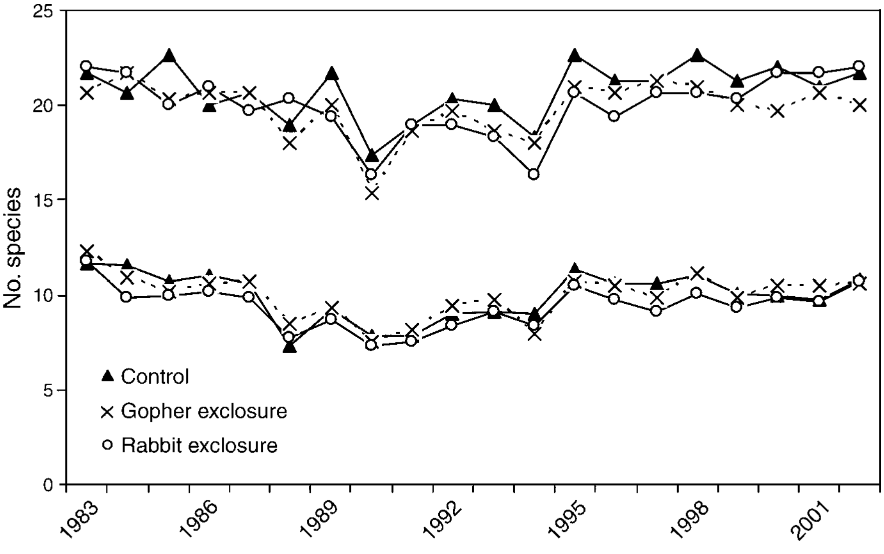

FIG. 8. Mean number of species per quadrat (lower set of lines, $n = 72$) and per treatment replicate quadrats (upper set of lines, $n = 3$) in each year, in control, gopher exclosure, and rabbit exclosure plots for the period 1983–2002.

2002, Wright and Jones 2006). Their activity has a pronounced impact on above- and belowground patterns and processes in the serpentine grassland (Hobbs and Hobbs 1987, Koide et al. 1987), as has also been indicated by studies of gophers and other fossorial rodents elsewhere (e.g., Klaas et al. 2000, Rebollo et al. 2002, Canals et al. 2003, Seabloom and Richards 2003). Our earlier studies examined the impacts of gophers in more detail (Hobbs and Mooney 1985, 1991, 1995), and our current study echoes some of the findings there: for instance, where gophers were successfully excluded for a number of years, the abundance of geophytes increased markedly. Since geophytes are a preferred food source for gophers, this finding is not surprising. On the other hand, our earlier work also suggested that gopher disturbance played an important role in maintaining overall species richness by providing sites with altered resource availability and reduced competition (Hobbs and Mooney 1985, Koide et al. 1987). The disturbance regime caused by gopher activity has been shown in the present study to be very variable both in space and in time. Total amounts of disturbance varied greatly from year to year, apparently not related in any simple way to rainfall variations. As has been found in other studies (Overton and Levin 2003, Gram et al. 2004), soil depth was highly variable in the experimental plots, and perhaps not surprisingly, gopher activity was more frequent in deeper soils compared with the shallower areas associated with rock close to the soil surface. We do not discuss the spatial variation in disturbance and grassland composition further here, but Overton and Levin (2003) concluded that plant species distributions could be partially explained by the patterns of soil depth and gopher disturbance, but that a large amount of the spatial patterning in species abundance remained unexplained.

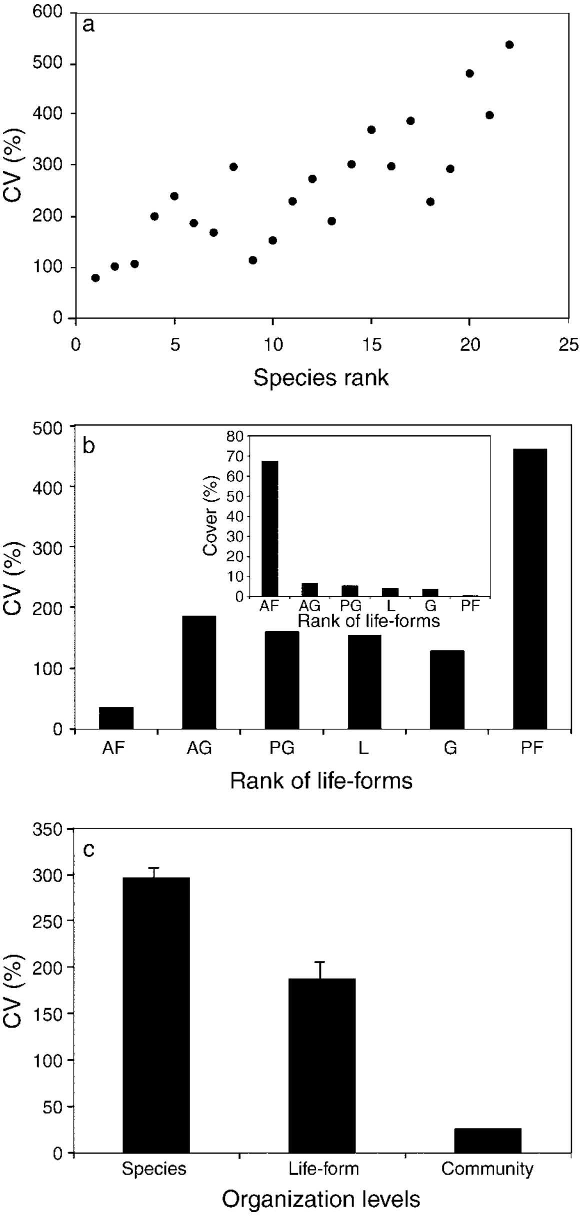

FIG. 9. Coefficients of variation (CV) in plant cover at different levels of organization. (a) Scatterplot of species-level CVs against relative cover-based species ranks (species that occurred only sporadically in the 20-year study period were omitted). (b) Relationship between CVs of life-forms and relative cover-based ranks of functional groups, with the inset showing the relative cover values of functional groups in descending order. Abbreviations are: AF, annual forbs; AG, annual grasses; PG, perennial grasses; L, legumes; G, geophytes; PF, perennial forbs. (c) Comparison of CVs (mean + SE) at the species, life-form, and community levels (means differ significantly at $P < 0.001$, as tested by t test).

Because the disturbance agent is an animal, the expression of the disturbance is tied to the behavior and population dynamics of the animal, about which we have limited information regarding the study site. More generally, *Thomomys bottae* is known to be solitary, with individual animals inhabiting separate tunnel networks (Lacey et al. 2000). Because of the metabolic expense of tunnel construction, existing tunnel networks are thought to be maintained over long periods and are taken over by dispersing individuals when the resident animal dies (Vleck 1981, Reichman et al. 1982). Hence, one can expect that certain areas of grassland are likely to be more frequently disturbed during ongoing maintenance of existing tunnel networks. This is certainly the case in the study plots, although our data also indicate that activities are also more widely dispersed on occasion, with none of the marked quadrats escaping disturbance entirely during the 20-year study period. As Seabloom and Richards (2003:2902) conclude, "...biotically-generated disturbances have the potential to generate spatially and temporally complex patterns of disturbance that shape plant–herbivore communities in ways that may be very distinct from abiotic disturbances." Our results support earlier findings that suggest that gopher activities have a significant impact on the patterning and composition of

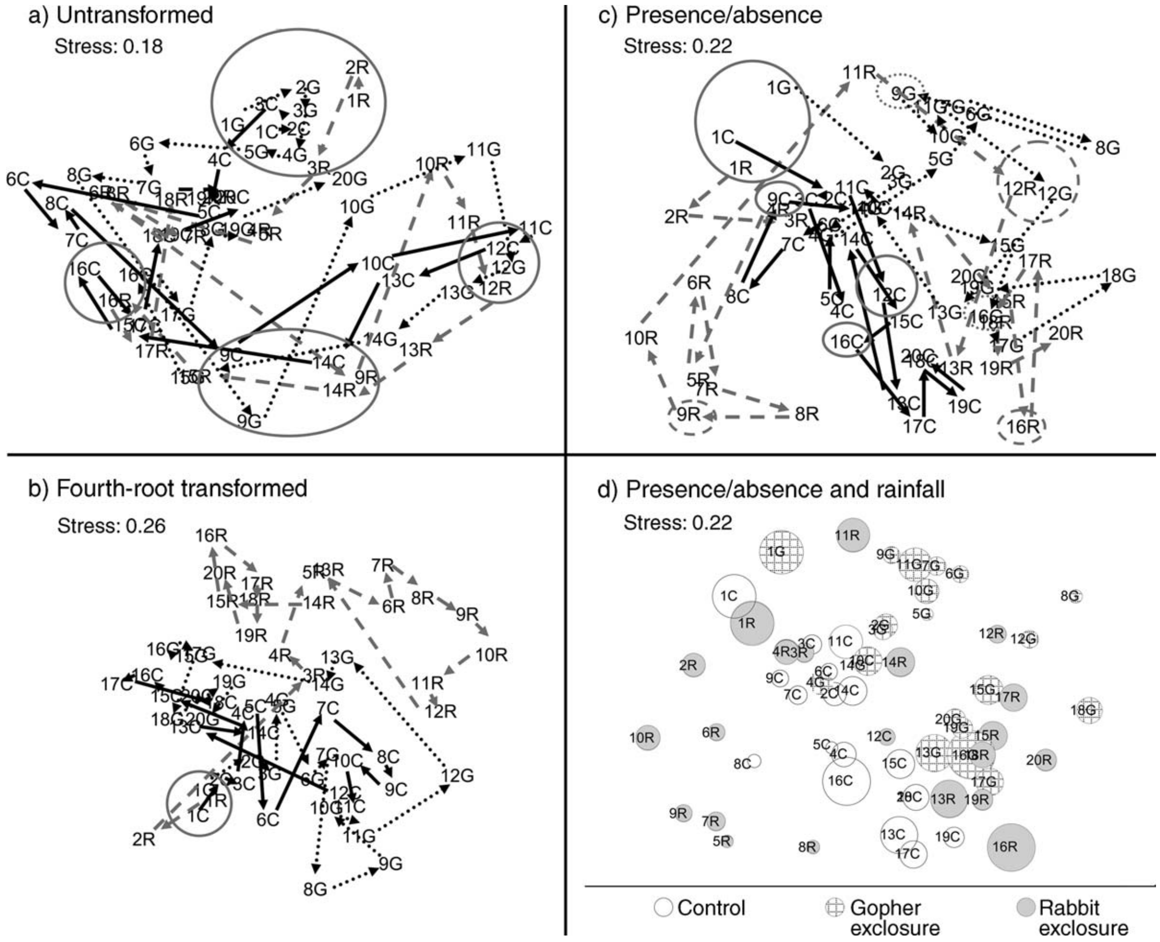

FIG. 10. Nonparametric multidimensional scaling ordination (first two axes) using PRIMER version 5.2 (Clarke and Warwick 2001), from an association matrix using Bray-Curtis similarity and no data standardization on species percent cover values (mean per treatment) over the period 1983–2002. Numbers 1–20 represent years 1983 through 2002. Abbreviations are: C, control; G, gopher exclosures; and R, rabbit exclosures. (a) No data transformation, years 1, 9, 12, and 16 are circled for clarity; (b) fourth-root transformation, year 1 circled; (c) ordination using presence/absence data, years 1, 9, 12, and 16 circled; (d) ordination using presence/absence data, with rainfall amount superimposed as bubbles (bubble size proportional to annual growing season rainfall total, from Fig. 1). Stress values indicate the extent to which the distances between points in the ordination represent a good fit with the similarities between points in the similarity matrix. Low stress values (below 0.2) indicate a good representation, while higher values indicate that the ordination cannot represent all relationships accurately. Values between 0.2 and 0.3 indicate that the ordination is of some interpretive value, but values over 0.3 indicate that the ordination should not be used to interpret data.

the grassland. The results further indicate that gopher activity most influences the abundances of the less common species and that impacts are most obvious where numerous repeat gopher disturbances occur.

Impact of aboveground herbivory

A further aspect of the distribution of gopher activity is the dramatic increase in disturbance within the aboveground exclosures. These plots experienced a marked increase in the frequency of gopher activity, which matches previous observations of an interaction between above- and belowground herbivores (Hunter 1991, Stromberg and Griffin 1996). It appears that this increase in gopher disturbance within the aboveground exclosures probably masked any potential treatment effect from the removal or reduction of aboveground herbivory. Often the impact of gopher disturbance was so pervasive in the plots that potential differences resulting from changes in aboveground herbivory were virtually undetectable. It is certainly clear from the analyses that the aboveground exclosures exhibited radically different dynamics from the other plots. In particular, the aboveground exclosures consistently showed lower abundances of perennial grasses and higher abundances of legumes. However, our experimental setup does not allow us to detect the relative roles of reduced aboveground herbivory and increased gopher activity; both the reduced perennial grass and increased legume abundance could be adequately explained by the increased gopher disturbance alone. This is a limitation of the study design, which was restricted due to space limitations imposed at the start of

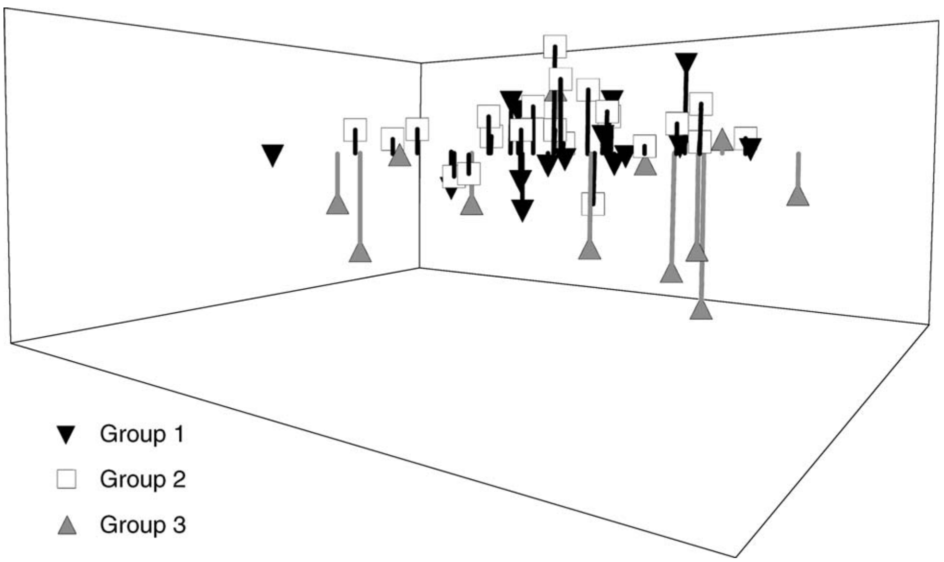

FIG. 11. Nonparametric multidimensional scaling ordination (first three axes) using PRIMER version 5.2 (Clarke and Warwick 2001), from an association matrix using Bray-Curtis similarity and no data standardization on species percent cover values of 2002 50 × 50 cm data from quadrats (in either control plots or gopher exclosures) disturbed different numbers of times over the period 1983–2002. Group 1 was disturbed twice in 20 years; group 2 was disturbed four times in 20 years; and group 3 was disturbed eight times in 20 years. The lines extending from the symbols indicate the major direction of variation among points, with the longer lines indicating a greater difference between group-3 points and the others.

the experiment and did not include a full above- and belowground exclosure treatment. The pervasive impact of gopher activity in the aboveground exclosures was not foreseen at the start of the experiment. From our experience during the study, it is unlikely that any exclosure would have remained uninvaded by gophers for prolonged periods, but the inclusion of a full exclosure treatment could have allowed some assessment of the relative roles of above- and belowground impacts.

Response of individual grassland species

A key finding is the variety of patterns of response to both rainfall and disturbance shown by individual species. Some species were ubiquitous in the grassland throughout most of the study but varied noticeably in local abundance, while others varied both in distribution and abundance, with some exhibiting phases of local presence and absence. In general, it appears that the abundance of the more dominant species is tied quite strongly to interannual rainfall variation, with some species becoming more abundant with increasing rainfall amounts and others showing the opposite pattern. While temporal patterns in species abundance can be related in a broad way to rainfall patterns via the multivariate analyses conducted, it has proven difficult to clearly demonstrate this relationship based on simple correlations with rainfall amounts in the current or previous years.

The variation in abundance of dominant species with rainfall broadly dictates the course-grain variations in grassland appearance from year to year. On the other hand, species with intermediate or low abundances in the grassland seem to be relatively less affected by variation in rainfall and respond more to the experimental manipulation of gopher disturbance and/or aboveground grazing. For instance, species such as *Agoseris heterophylla*, *Castilleja densiflora*, and *Hemizonia congesta* var. *luzulaefolia* and all the perennial grasses are clearly sensitive to increasing levels of gopher disturbance. The effects of treatments nevertheless appear to be clearest in low-rainfall years (Fig. 10d), and many less abundant species show significant correlations with rainfall amounts (Table 3), indicating that rainfall and treatment interact.

In addition, dominant species are also locally impacted by gopher disturbance, as has been demonstrated here and in previous studies (Hobbs and Mooney 1985), but our results have helped untangle the interactions between this disturbance and rainfall variation and indicated that these factors differentially influence the dominant and rarer species.

In addition to these overall trends, there are a number of important observations regarding individual species. First, several species indicated considerable variation in distribution and/or abundance over the study period. This was most marked in *Microseris douglasii*, which was a common occurrence earlier in the study but rarely reached high levels of abundance. It increased dramatically in frequency and abundance between 1992 and 1997 to become one of the dominant community components during that time, before declining markedly thereafter. Similar but less dramatic variations can be seen in other species, such as *Hesperevax sparsiflora* and *Hemizonia congesta* var. *luzulaefolia*. Changes in species abundances through time are a feature of other grassland ecosystems that have been the subjects of long-term studies such as the Park Grass Experiment in England (Dodd et al. 1995, Silvertown et al. 2006) and elsewhere (e.g., Tilman and El Haddi 1992, van der Maarel and Sykes 1993, 1997, Sykes et al. 1994, Stampfli and Zeiter 2004). The mechanisms driving these changes in abundance have rarely been clearly demonstrated, although the studies by Tilman and El Haddi (1992) and Stampfli and Zeiter (2004) both documented changes following drought episodes. Tilman and El Haddi (1992) noted that drought resulted in loss of annual species in grassland and marked declines in local species richness and that the species did not necessarily return in the period after the drought. In contrast, the species in our study all seem to indicate an ability to persist during an extended drought period or return thereafter, and overall species numbers returned to pre-drought levels relatively quickly (Fig. 8).

Evidence for the "insurance hypothesis"

Our results have important implications when questions of species' roles in ecosystem function are considered. There has been considerable debate and ongoing research in this area (Loreau et al. 2001, 2002*b*, Spehn et al. 2005). While there have been detailed experimental studies investigating the relationships among species composition, diversity, and ecosystem functioning in serpentine grassland (Hooper and Vitousek 1997, 1998, Hooper 1998), these have been relatively short-term and hence have been conducted within a relatively small band of the known environmental variation. Our current study yields some important insights into the biodiversity–ecosystem function debate by providing clear field evidence in support of what has become known as the "insurance hypothesis." This hypothesis proposes that different species (or phenotypes) respond differently to environmental changes, which allows functional compensations among species and hence a more predictable aggregate community or ecosystem response (Yachi and Loreau 1999, Loreau et al. 2002*a*). Species that may apparently be functionally redundant at a particular time may potentially become more important when environmental conditions are different.

This hypothesis has received increasing theoretical attention (Naeem 1998, Ives et al. 1999*a*, *b*, Yachi and Loreau 1999, Loreau 2000) and has been supported by microcosm experiments (McGrady-Steed et al. 1997, Naeem and Li 1997) and indicative short-term field observations (Walker et al. 1999). However, there have been few empirical field studies that have yielded clear supporting evidence. In our study, we have been able to replicate the findings of Bai et al. (2004) and have shown that the variability in the overall plant community (in terms of plant cover) is considerably less than that for life-form groups, which is in turn much less than that for individual species. This can be interpreted as illustrating that, while individual species abundances vary greatly over the study period, the level of variation declines with increasing levels of aggregation. Hence species compensation effects reduce the level of variation in life-form groups, and in turn the overall degree of variation for the entire community is much lower. In other words, overall plant community cover is maintained at a relatively constant level despite large variations in the constituent species.

We were able to include a much higher percentage of the overall number of plant species present than in Bai et al.'s (2004) study and were also able to compare the impacts of different disturbance regimes (although no obvious differences due to treatment were detected). As in Bai et al.'s (2004) study, we found that the coefficient of variation increased from common to rarer species, but we did not find a similar trend for life-form groups. In our study, annual grasses and, to a lesser extent, perennial grasses showed more variability than would be expected on the basis of their rank based on relative abundance. This probably reflects the dramatic increases and declines in abundances of all grass species seen over the period of the study. This contrasts with the annual forb group, within which large variations are seen for individual species but overall abundance of the group remains fairly similar throughout.

There is clear evidence for temporal complementarity in the forbs with, in particular, *Microseris douglasii* moving from being a relatively minor component of the plant community at the start of the study to being a major dominant following a period of prolonged drought. This lends support to the idea that species diversity provides resilience or "insurance" through time and indicates the danger of attaching relative functional significance to particular species following one-off or short-term observations or experiments.

Invasion by nonnative grasses

One of the most noticeable features of the data set is the invasion of the serpentine grassland by the nonnative grass *Bromus hordeaceus*. The serpentine grassland has remained relatively free of the nonnative grasses, mostly of Mediterranean origin, that dominate most California grasslands, mainly because of the low nutrient status and chemical composition of the serpentine soils (Kruckeberg 1954, McNaughton 1968, Huenneke et al. 1990, Streit et al. 1993). Previous studies have indicated that invasion is promoted either when nutrient availability is increased experimentally (Hobbs et al. 1988, Huenneke et al. 1990) or in response to NO_x pollution (Weiss 1999) and also in response to episodically high rainfall events (Hobbs and Mooney 1991, 1995). This fits with the idea that short-term enhancements of resource availability can enhance community invasibility (Davis et al. 2000, Gross et al. 2005). The long-term data presented here clearly track the invasion of the grassland by *B. hordeaceus* following the 1982–1983 El Niño event and again following the 1997–1998 event. It is interesting to note that *B. hordeaceus* abundance reached a peak several years after the El Niño event in both cases and that it started to increase in frequency prior to the 1997–1998 event, possibly in response to the higher rainfall in 1994–1995 season.

It is also interesting to examine not just the trigger for the invasion but also the possible reasons for the sudden decline of *B. hordeaceus* following the invasion that commenced in 1984. The grass reached peak abundance in 1986 but then abundance fell dramatically in 1987. This coincided with the 1986–1987 rainfall season that was marked by a period of heavy rain in September followed by a pronounced period without further rain and the lowest total rainfall amount recorded during this study. Observations suggested that *B. hordeaceus* germinated in abundance following the September rains, but subsequently failed to survive during the ensuing period without significant further rain. It is interesting to speculate that, without this check on *B. hordeaceus* populations, the species may have persisted at high levels of abundance for considerably longer despite overall lower rainfall amounts. Ongoing analysis of the experiment will reveal whether this happens following the second invasion starting in the late 1990s.

Invasion by *B. hordeaceus* and other nonnative grasses significantly alters the serpentine grassland by forming dense patches within which few native species survive and leaving a persistent thatch that prevents further recolonization by native species and alters the local nutrient dynamics (Hobbs et al. 1988, Huenneke et al. 1990, Weiss 1999). Competition from nonnative species has also been shown to impact negatively native perennial bunchgrass species such as *Nasella pulchra* in other California grasslands (Dyer and Rice 1999, Brown and Rice 2000, Corbin and D'Antonio 2004). The invasion process may also be enhanced by increasing levels of nitrogen input. While this process can be interrupted by gopher disturbance, there is a risk that long-term dominance by *B. hordeaceus* could significantly reduce the grassland diversity locally. From a management perspective, in a situation such as Jasper Ridge Biological Preserve, it will be important to monitor the situation carefully and perhaps consider initiating interventive management such as seasonal grazing or mowing to reduce nonnative grass abundance.

Value of the long-term data set

Results from this long-term study have provided important insights into the dynamics of a grassland community in relation to climatic variability and varying disturbance regimes. This in turn has provided information that is relevant to many topics of current concern in ecology, such as biodiversity–function relationships, invasion ecology, and the impacts of global change.

The value of long-term experiments and data sets has often been discussed (e.g., Likens 1989, Burt 1994, Southwood 1994, Silvertown et al. 2006, Walther 2007), and it is clear that the longer the study can be, the greater the insight into the dynamics of the study system that is possible. Not only is it possible to unearth long-term trends and responses to climatic and other environmental variation, but it also becomes possible to place shorter-term studies in a longer-term context. As an example, a recent study (Peters et al. 2005) compared the results of several previous investigations into the impacts of the harvester ant *Messor andrei* on serpentine grassland (Roberts 1970, Hobbs 1985, Brown and Human 1997), conducted further field analyses, and noted marked differences in the results obtained by the different studies. These studies, conducted in 1970, 1984, 1989, and 1994–1996 reached differing conclusions concerning the species selected by ants, the impact of harvesting on local plant abundances, and hence the overall impact of the ants on grassland composition and dynamics.

While we cannot examine the 1970 results further, we can consider the results from 1984, 1989, and 1994–1996 in the context of the long-term data presented here. Clearly, the sampling periods represent markedly different situations with respect to rainfall amount and distribution in both the actual years sampled and in the years leading up to that. The 1984 sample immediately follows years of very high rainfall, while the 1989 sample follows a number of drier years, and the 1994–1996 period spans a higher rainfall period. The sampling periods also are characterized by very different relative abundances of many of the key species found to be harvested by the ants. While the data presented in each of the four publications cited above does not allow a detailed cross-comparison of ant preferences relative to plant abundance in the overall community, the long-term data provide some indication that the differences in vegetation composition may be reflected in differences in ant behavior and relative impact. That four different studies conducted over a 25-year period arrived at markedly different conclusions indicates the problems with trying to generalize from short-term studies.

This is further reinforced when one considers attempts to model the dynamics of the serpentine grassland based on short-term observations. Attempts to model the spatial and temporal dynamics of the grassland in relation to disturbance (e.g., Hobbs and Hobbs 1987, Moloney et al. 1992, Wu and Levin 1994, Moloney and Levin 1996) have all been based on the plant population parameters derived from a short-term study conducted during 1983–1984 (Hobbs and Mooney 1985). As has been indicated above, the grassland composition during that period has not been replicated again over the 20-year study and one of the key species modeled, *Bromus hordeaceus*, was mostly absent from the study plots for several of the study years. Other results have indicated that the dynamics of reinvasion of recent gopher mounds varies greatly from year to year (Hobbs and Norton 2004), with different species colonizing more strongly and different total numbers of plants colonizing from year to year. Once again, therefore, the need for caution in interpreting modeling results is highlighted, as is the need to replicate shorter-term intensive studies at different times and under differing rainfall regimes.

All of the above becomes increasingly important when we attempt to understand what might happen to the grassland ecosystem, or indeed any other ecosystem, under future global change scenarios. Changes in climate, disturbance regime, and nutrient inputs may all have important effects on both the serpentine grassland ecosystem and many other ecosystems worldwide. Detailed short-term experiments can greatly assist with unravelling the interactive effects of changing environmental conditions (e.g., Shaw et al. 2002, Zavaleta et al. 2003*a*, *b*) and the functional implications of species loss and addition (e.g., Hooper and Vitousek 1997, 1998, Hooper 1998). However, the results from these experiments can be supplemented by relatively inexpensive ongoing recording of long-term field plots such as those reported here. Continued recording of data in the experimental plots is currently being used to test hypotheses arising from the first 20 years of the study and will be the subject of future publications.

ACKNOWLEDGMENTS

The experimental plots reported on here were initially set up while R. J. Hobbs held a NATO postdoctoral fellowship through the U.K. Natural Environment Research Council. Subsequent support has included funding from the National Science Foundation, Mellon Foundation, CSIRO, and Murdoch University. We thank the many people involved in the construction and upkeep of the experimental exclosures, those who provided periodic assistance with field sampling, and Jasper Ridge Biological Preserve for permission to continue the work there. We also thank Colin Yates and Neil Gibson for advice on statistical analyses and data management respectively, two anonymous referees for constructive comments on the draft manuscript, and the many people with whom we have discussed this work over the years.

LITERATURE CITED

Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. Oikos 116:221–232.

Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolian grassland. Nature 431:181–184.

Brown, C. S., and K. J. Rice. 2000. The mark of Zorro: effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. Restoration Ecology 8:10–17.

Brown, M. J. F., and K. G. Human. 1997. Effects of harvester ants on plant species distribution and abundance in a serpentine grassland. Oecologia 112:237–243.

Burt, T. P. 1994. Long-term study of the natural environment—Perceptive science or mindless monitoring? Progress in Physical Geography 18:475–496.

Canals, R. M., D. J. Herman, and M. K. Firestone. 2003. How disturbance by fossorial mammals alters N cycling in a California annual grassland. Ecology 84:875–881.

Chapin, F. S. I., O. E. Sala, and E. Huber-Sanwald, editors. 2001. Global biodiversity in a changing environment: scenarios for the 21st century. Springer, New York, New York, USA.

Chesson, P., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253.

Clarke, K. R., and R. N. Gorley. 2001. PRIMER v5: user manual/tutorial. Primer-E, Plymouth, UK.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Second edition. Primer-E, Plymouth, UK.

Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historic invasion. Ecology 85:1273–1283.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Davis, M. A., et al. 2005. Vegetation change—a reunifying concept in plant ecology. Perspectives in Plant Ecology, Evolution, and Systematics 7:69–76.

Dodd, M., J. Silvertown, K. McConway, J. Potts, and M. Crawley. 1995. Community stability: a 60-year record of trends and outbreaks in the occurrence of species in the Park Grass Experiment. Journal of Ecology 83:277–285.

Dukes, J. S., and B. A. Hungate. 2002. Elevated carbon dioxide and litter decomposition in California annual grasslands: Which mechanisms matter? Ecosystems 5:171–183.

Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. Ecology 80:2697–2710.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

Ehrlich, P. R., and D. D. Murphy. 1987. Conservation lessons from long-term studies of checkerspot butterflies. Conservation Biology 1:122–131.

Glantz, M. H. 2001. Currents of change: impacts of El Niño and La Niña on climate and society. Cambridge University Press, Cambridge, UK.

Goldberg, D., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. Journal of Ecology 85:409–418.

Gram, W. K., E. T. Borer, K. L. Cottingham, E. W. Seabloom, V. L. Boucher, L. Goldwasser, F. Micheli, B. E. Kendall, and R. S. Burton. 2004. Distribution of plants in a California serpentine grassland: Are rocky hummocks refuges for native species? Plant Ecology 172:159–171.

Greenland, D., D. G. Goodin, and R. C. Smith, editors. 2003. Climate variability and ecosystem response at long-term ecological research sites. Oxford University Press, New York, New York, USA.

Gross, K. L., G. G. Mittelbach, and H. L. Reynolds. 2005. Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. Ecology 86:476–486.

Haddad, N. M., D. Tilman, and J. M. H. Knops. 2002. Long-term oscillations in grassland productivity induced by drought. Ecology Letters 5:110–120.

Hickman, J. C., editor. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California, USA.

Hobbs, R. J. 1985. Harvester ant foraging and plant species distribution in annual grassland. Oecologia 67:519–523.

Hobbs, R. J., S. L. Gulmon, V. J. Hobbs, and H. A. Mooney. 1988. Effects of fertiliser addition and subsequent gopher disturbance on a serpentine annual grassland community. Oecologia 75:291–295.

Hobbs, R. J., and V. J. Hobbs. 1987. Gophers and grassland: a model of vegetation response to patchy soil disturbance. Vegetatio 69:141–146.

Hobbs, R. J., and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. Oecologia 67:342–351.

Hobbs, R. J., and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. Ecology 72:59–68.

Hobbs, R. J., and H. A. Mooney. 1995. Spatial and temporal variability in California annual grassland: results from a long-term study. Journal of Vegetation Science 6:43–57.

Hobbs, R. J., and H. A. Mooney. 1996. Effects of episodic rainfall events on Mediterreanean-climate ecosystems. Pages 71–85 *in* J. Roy, J. Aronson, and F. di Castri, editors. Timescales in biological responses to water constraints. SPB Academic, Amsterdam, The Netherlands.

Hobbs, R. J., and D. A. Norton. 2004. Ecological filters, thresholds and gradients in resistance to ecosystem reassembly. Pages 72–95 *in* V. M. Temperton, R. J. Hobbs, T. J. Nuttle, and S. Halle, editors. Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, D.C., USA.

Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutierrez, and G. M. J. Mohren. 2001. El Nino effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16: 89–94.

Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. Ecology 79:704–719.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecological Monographs 68:121–149.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Calfornian serpentine grassland. Ecology 71:478–491.

Hunter, J. E. 1991. Grazing and pocket gopher abundance in a California annual grassland. Southwestern Naturalist 36: 117–118.

Huxman, T. E., K. A. Snyder, D. Tissue, A. J. Leffler, K. Ogle, W. T. Pockman, D. R. Sandquist, D. L. Potts, and S. Schwinning. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253.

Ives, A. R., K. L. Gross, and J. L. Klug. 1999*a*. Stability and variability in competitive communities. Science 286:542–544.

Ives, A. R., J. L. Klug, and K. L. Gross. 1999*b*. Stability and species richness in complex communities. Ecology Letters 3: 399–411.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Klaas, B. A., K. A. Moloney, and B. J. Danielson. 2000. The tempo and mode of gopher mound production in a tallgrass prairie remnant. Ecography 23:246–256.

Klein Tank, A. M. G., et al. 2002. Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. International Journal of Climatology 22:1441–1453.

Koide, R. T., L. F. Huenneke, and H. A. Mooney. 1987. Gopher mound soil reduces growth and affects ion uptake of two annual grassland species. Oecologia 72:284–290.

Kruckeberg, A. R. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. Ecology 35:267–274.

Lacey, E. A., J. L. Patton, and G. N. Cameron, editors. 2000. Life underground: the biology of subterranean rodents. University of Chicago Press, Chicago, Illinois, USA.

Likens, G. E., editor. 1989. Long-term studies in ecology: approaches and alternatives. Springer Verlag, New York, New York, USA.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3–17.

Loreau, M., A. Downing, M. Emmerson, A. Gonzalez, J. Hughes, P. Inchausti, J. Joshi, J. Norberg, and O. Sala. 2002*a*. A new look at the relationship between diversity and stability. Pages 79–91 *in* M. Loreau, S. Naeem, and P. Inchausti, editors. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, UK.

Loreau, M., S. Naeem, and P. Inchausti, editors. 2002*b*. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, UK.

Loreau, M., et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808.

McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. Nature 390: 162–164.

McNaughton, S. J. 1968. Structure and function in California grasslands. Ecology 49:962–972.

McPhaden, M. J., S. E. Zebiak, and M. H. Glantz. 2007. ENSO as an integrating concept in earth science. Science 314:1740–1745.

Moloney, K. A., and S. A. Levin. 1996. The effects of disturbance architecture on landscape-level population dynamics. Ecology 77:375–394.

Moloney, K., S. A. Levin, N. R. Chiariello, and L. Buttel. 1992. Pattern and scale in a serpentine grassland. Theoretical Population Biology 41:257–276.

Morecroft, M. D., G. J. Masters, V. K. Brown, I. P. Clarke, M. E. Taylor, and A. T. Whitehouse. 2004. Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. Functional Ecology 18: 648–655.

Munz, P. A., and D. D. Keck. 1968. A California flora and supplement. University of California Press, Berkeley, California, USA.

Murphy, D. D., and S. B. Weiss. 1988. Ecological studies and the conservation of the bay checkerspot butterfly, *Euphydryas editha bayensis*. Biological Conservation 46:183–200.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology 12:39–45.

Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390:507–508.

Overton, J. M., and S. A. Levin. 2003. Components of spatial patterning in a serpentine grassland. Ecological Research 18: 405–421.

Peters, H. A., N. R. Chiariello, H. A. Mooney, S. A. Levin, and A. E. Hartely. 2005. Native harvester ants threatened with widespread displacement exert localized effects on serpentine grassland plant community composition. Oikos 109:351–359.

Rebollo, S., L. Pérez-Camacho, J. Valencia, and A. Gomez-Sal. 2002. Vole mound effects and disturbance rate in a mediterranean plant community under different grazing and irrigation regimes. Plant Ecology 169:227–243.

Reichman, O. J., and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution 17:44–49.

Reichman, O. J., T. G. Whitham, and G. A. Ruffner. 1982. Adaptive geometry of burrow spacing in two pocket gopher populations. Ecology 63:687–695.

Roberts, J. 1970. The impact of the harvester ant *Veromessor andrei* on plant reproduction on a serpentine outcrop. Thesis. Stanford University, Stanford, California, USA.

Scher, A. A., D. E. Goldberg, and A. Novoplansky. 2004. The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. Oecologia 141:353–362.

Schwinning, S., O. Sala, M. E. Loik, and J. R. Ehleringer. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141:191–193.

Seabloom, E. W., and S. A. Richards. 2003. Multiple stable equilibria in grasslands mediated by herbivore population dynamics and foraging behavior. Ecology 84:2891–2904.

Shaw, M. R., E. S. Zavaleta, N. R. Chiariello, E. E. Cleland, H. A. Mooney, and C. B. Field. 2002. Grassland responses to global environmental changes suppressed by elevated CO_2. Science 298:1987–1990.

Silvertown, J., M. Dodd, K. McConway, J. Potts, and M. Crawley. 1994. Rainfall, biomass variation, and community composition in the Park Grass Experiment. Ecology 75:2430–2437.

Silvertown, J., P. Poulton, E. Johnston, G. Edwards, M. Heard, and P. M. Bliss. 2006. The Park Grass Experiment 1856–2006: its contribution to ecology. Journal of Ecology 94:801–814.

Southwood, T. R. E. 1994. The importance of long-term experimentation. Pages 3–8 *in* R. A. Leigh and A. E. Johnston, editors. Long-term experiments in agricultural and ecological sciences. CAB International, Wallingford, UK.

Spehn, E. M., et al. 2005. Ecosystem effects of biodiversity manipulations in European grassland. Ecological Monographs 75:37–63.

Stampfli, A., and M. Zeiter. 2004. Plant regeneration directs changes in grassland composition after extreme drought: a 13 year study in southern Switzerland. Journal of Ecology 92: 568–576.

Streit, B., R. J. Hobbs, and S. Streit. 1993. Plant distributions and soil chemistry at a serpentine/non serpentine boundary. Pages 168–178 *in* B. Markert, editor. Plants as biomonitors: indicators for heavy metals in the terrestrial environment. VCH, Weinheim, Germany.

Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications 6:1189–1211.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

Sykes, M. T., E. van der Maarel, R. K. Peet, and J. H. Willems. 1994. High species mobility in species-rich plant communities: an intercontinental comparison. Folia Geobotanica Phytotaxa Praha 29:439–448.

Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. Oecologia 89:257–264.

Valentini, R., J. A. Gamon, and C. B. Field. 1995. Ecosystem gas exchange in a California grassland: seasonal patterns and implications for scaling. Ecology 76:1940–1952.

van der Maarel, E., and M. T. Sykes. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. Journal of Vegetation Science 4:179–188.

van der Maarel, E., and M. T. Sykes. 1997. Rates of small-scale species mobility in alvar limestone grassland. Journal of Vegetation Science 8:199–208.

Vleck, D. 1981. Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. Oecologia 49:391–396.

Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2: 95–113.

Walther, G.-R. 2007. Tackling ecological complexity in climate impact research. Science 315:606–607.

Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conservation Biology 13:1476–1486.

Weltzin, J. F., and G. R. McPherson, editors. 2003. Changing precipitation regimes and terrestrial systems. University of Arizona Press, Tuscon, Arizona, USA.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209.

Wu, J., and S. A. Levin. 1994. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. Ecological Monographs 64:447–464.

Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences (USA) 96:1463–1468.

Zavaleta, E. S., M. R. Shaw, N. R. Chiariello, H. A. Mooney, and C. B. Field. 2003*a*. Additive effects of simulated climate changes, elevated CO_2, and nitrogen deposition on grassland diversity. Proceedings of the National Academy of Sciences (USA) 100:7650–7654.

Zavaleta, E. S., M. R. Shaw, N. R. Chiariello, B. D. Thomas, E. E. Cleland, C. B. Field, and H. A. Mooney. 2003*b*. Responses of a California annual grassland community to three years of experimental climate change, elevated CO_2, and N deposition. Ecological Monographs 73:585–604.