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Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance

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Summary. This study examines the effects of soil disturbance by gophers on patterns of species abundance in an annual grassland community on serpentine soil. We assessed production, dispersal and storage of seed, germination, survivorship and growth of the most abundant species in undisturbed vegetation and on gopher mounds. Fewer seeds of the dominant species were dispersed onto gopher mounds due to the limited movement of seeds from within the closed vegetation. Species with taller flowering stalks were more likely to colonise gopher mounds. The timing of gopher disturbance in relation to the timing of seed fall determined which species could colonise mounds. Lower numbers of seeds falling onto gopher mounds resulted in lower seedling densities of several species compared with undisturbed areas. Survivorship of the commonest species differed between undisturbed areas and gopher mounds formed at different times of year. This resulted in characteristic spectra of species abundance on the different microhabitats, giving rise to distinct spatial patterning in the community. Plants growing on gopher mounds were generally larger and produced more seed than plants in undisturbed vegetation. We suggest that continued gopher disturbance is a factor allowing several species, including perennial grasses, to persist in this community.

The field of plant population ecology has attracted much research in recent years, and has provided considerable information on the dynamics of natural plant populations (Harper 1977; Silvertown 1982; Dirzo and Sarukhan 1984). Many studies have followed populations of an individual species through time, these often being species which exist as almost monospecific stands. The study of single species becomes more difficult in multi-species communities since interactions with other species may be important. Nevertheless, to achieve an understanding of community dynamics beyond the purely descriptive level we require information on the populations making up the community. Sharitz and McCormick (1973) were among the first to perceive the need for such information, and van der Maarel (1984) has recently reemphasised the need for greater interchange between studies at the population and community levels. Law (1981) has also emphasised the need for considering spatial as well as temporal dynamics of populations. This study is therefore an attempt to explain the dynamics and spatial patterning of a plant community by studying the population dynamics of the main constituent species. In particular, we try to relate spatial dynamics to the disturbance regime imposed by herbivore activity.

The study was carried out in an annual grassland on serpentine soil in Northern California. The serpentine soil in the study area has a very low nutrient status, low Ca:Mg ratio and elevated heavy metal concentrations. This combination of factors has evidently prevented non-native grasses (which dominate most California grasslands) from invading the serpentine outcrops which instead support a community characterised by a relatively high diversity of native forbs and some perennial bunchgrasses (McNaughton 1968). The only non-native species present in any abundance on the serpentine is the annual grass *Bromus mollis* L.

The grassland community is very spatially heterogeneous, with marked shifts in species dominance over very short distances. Some of this heterogeneity may be explained by variations in soil depth, more deeply rooted species being restricted to deeper pockets of soil (Gulmon et al. 1983). However, a further source of small-scale habitat variation may be found in the activities of western pocket gophers (*Thomomys bottae* Mewa) which are abundant on the serpentine outcrops. Procter and Whitten (1971) studied the population of *T. bottae* at our study site and concluded that numbers were relatively high on the serpentine because of the presence of high densities of *Brodiaea* spp., the corms of which are a preferred food. Other studies of *T. bottae* indicate, however, that gophers eat a wide range of plant material, both above- and below-ground (Fitch and Bentley 1949; Howard and Childs 1959; Gettinger 1984). No attempt is made here to assess the effect of this direct herbivory on the grassland community; rather, we concentrate on the effect of gophers in soil disturbance. These fossorial mammals dig tunnels 10–20 cm beneath the soil surface and periodically bring the excavated soil material to the surface, forming mounds of bare soil 30–50 cm in diameter. This excavated material buries any existing vegetation to a depth of up to 10 cm. Gophers may be active throughout the year, although their activity declines during summer when the soil dries out (Miller 1948). We estimate that they can turn over as much as 30% of the total area per annum (Gulmon and Hobbs unpublished).

We hypothesised, therefore, that this continual soil turn-

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over by gophers exerts a strong influence on the spatial and temporal dynamics of the grassland community. Numerous other studies in a variety of vegetation types have indicated that gopher activity may have pronounced effects on production and community composition (e.g. Ellison and Aldous 1952; Mielke 1977; Foster and Stubbendieck 1980). Tilman (1983) has also recently suggested that gophers may be an important determinant of the rate of succession and community diversity. Here we report an attempt to follow the population dynamics of the major species present in relation to gopher disturbance. We present data on seed production and storage, and we follow the processes of seed dispersal and subsequent seedling establishment and survival in areas undisturbed by gopher activity and on gopher mounds formed at different times of the year.

Methods

Study site

All studies were carried out on Jasper Ridge Biological Preserve, close to Stanford University in San Mateo County, N. California. The reserve comprises a low-lying ridge (max. elevation 189 m) on the eastern side of the Santa Cruz mountains. A serpentine outcrop bisects the ridge. The vegetation on the serpentine and adjacent non-serpentine soils has been described by McNaughton (1968). The climate is a Mediterranean-type with a mean annual rainfall of 480 mm and a virtually rain-free period from May to September. Growth of the annual plants commences after the first significant rains at the end of summer. Growth is slow during the winter months and increases as the temperatures increase in Spring. Flowering and seeds are completed for most species by April or May, after which the plants die. However, a few deeper-rooted annual species, notably the tarweeds *Calycadenia multiglandulosa* DC. and *Hemizonia luzulifolia* DC., flower later in the summer, as do the perennial grasses.

Community composition and spatial patterning

Thirty-six 50 × 50 cm quadrats were taken at random within the study area in April 1983, and cover of each species present within the quadrats estimated by eye. To establish the spatial patterning of the major species, 5 transects, each 4 m long by 10 cm wide, were taken through the vegetation, and cover of each species within 40 10 × 10 cm quadrats was estimated along each transect. In addition the mean sizes of bare gopher mounds were estimated by measuring two perpendicular diameters on each of 20 mounds. Diameters of grass clumps or patches were measured in a similar manner.

Seed production

Numbers of seeds produced per unit area were estimated for each species in undisturbed areas from the number of flowers/inflorescences per m^2 (calculated from ten 50 × 50 cm quadrats) and the mean number of seeds per flower or inflorescence (found from 25 individuals of each species). For convenience, propagules will be referred to as seeds throughout this paper, although the structure involved for some species may in fact be fruits.

Seed rain

We used sticky traps to obtain an estimate of the numbers of seeds of each species falling within undisturbed areas and onto recently-formed gopher mounds. The traps were 5 cm diameter petri dishes with filter paper coated in 'Tanglefoot' and covered with 1 cm mesh wire netting. Twenty-five traps were placed on recently formed gopher mounds and 25 within adjacent undisturbed vegetation, in April 1983 before seedfall commenced. Seeds found in the traps were counted and removed once a week until November 1983. Possible seed predation in the traps was tested for by putting out similar traps containing known numbers of seeds and re-counting these after one week.

Seed dispersal

To obtain information on distances over which seeds are dispersed within the undisturbed grassland vegetation, we attempted to mark all seeds produced within an area 50 cm in diameter and to estimate distances travelled by marked seeds. Seeds of *Lasthenia californica* D.C. ex Lindley, *Agoseris heterophylla* (Nutt.) Greene and *Microseris douglasii* (D.C.) Sch. – Bip. were marked by coating the ends of the pappus with red ink before the seed head opened fully. Seeds of *Bromus mollis* and *Vulpia microstachys* (Nutt.) Benth var. *pauciflora* (Beal) Lonard and Gould were similarly marked on the awns. Seeds of *Plantago erecta* Morris could not be marked since they remain enclosed until release. Sticky traps (as above) were placed on 6 radii (60° apart) from the centre of the marked area at 12.5 cm intervals to a distance of 125 cm from the centre. This gave 10 traps on each radius, 2 of which were within the marked area. The traps were checked at weekly intervals from April to September 1983 and marked and unmarked seeds were counted and removed.

Seed storage

We estimated numbers of seeds present at various depths in the soil at different times of year by observing germination from soil samples in the greenhouse. Samples were collected at 2 month intervals from October 1983 to December 1984. At each collection, 25 samples were taken at 4 soil depths (0–1 cm, 1–2 cm, 5–6 cm, 10–11 cm) using a corer of dimensions 2.5 × 2.5 × 1 cm to extract samples laterally from an excavated soil face. We used this method to reduce the possibility of seed movement with the profile due to sampling disturbance. Samples were taken from beneath undisturbed vegetation and from gopher mounds. All samples were placed in the greenhouse in pots 6 cm in diameter filled with washed sand. These were watered regularly, and germinated seedlings were counted and removed after identification over a period of 8 weeks.

Germination, survivorship, growth and fecundity

In October 1983 we set up permanent 10 × 10 cm quadrats within undisturbed vegetation, on gopher mounds formed in April 1983 and on mounds formed in July 1983 (10 quadrats in each microhabitat). These quadrats were inspected at weekly intervals from October to December 1983, and thereafter monthly until June 1984. All individuals appearing in the quadrats were mapped using a co-ordinate system and the survival of all individuals was followed. After seed set in April 1983 all seed heads of all species (except *Calycadenia multiglandulosa*) were collected and numbers of seeds produced by each plant were determined. *Calycadenia* seed heads were collected in June. In addition, 10 complete individuals of each of the major species growing on each of the three microhabitats described above (but outside the quadrats) were collected before seed set, dried and weighed.

Results and discussion

Community composition and spatial patterning

Mean percentage cover values and frequency of occurrence for the species present at the study site are given in Table 1. *Lasthenia californica, Plantago erecta* and *Calycadenia multiglandulosa* are the most abundant species in this location, with other common species being the grasses *Bromus mollis* and *Vulpia microstachys* var. *pauciflora* and several Asteraceae (These species are referred to by their generic names only throughout the rest of this paper, unless ambiguity arises; full names are given in Table 1). These measurements were made in April and it should be noted that the perennial grasses assume greater importance later in summer.

Figure 1 illustrates the nature of two transects taken through the study area. For clarity, only data for *Lasthenia, Bromus* and the perennial bunchgrass (*Stipa* and *Sitanion*) are shown here. Figure 1a shows a typical pattern found in the grassland, with areas dominated almost completely by *Lasthenia* (and *Plantago*) punctuated by areas of lower abundance of these species and increased cover of *Bromus*. Figure 1b shows an area where perennial bunchgrasses are abundant, and reveals a similar pattern of *Lasthenia* dominance with localised patches of grass. However, the bunchgrass are not individual plants but are composed of several individuals of different species (*Stipa* and *Sitanion* here). Mean diameters of patches of *Bromus* and of perennial grasses were 45.0+3.4 cm and 37.0+2.0 cm respectively. The mean diameter of newly-formed gopher mounds was found to be 37.6+1.7 cm). These mean diameter values are not significantly different from one another (using the t-test) and this led us to hypothesise that gopher activity may be responsible for the observed patterns of species abundance.

Seed production and seed rain

Numbers of seeds produced per m^2 in undisturbed vegetation are given in Table 2, along with the total number of seeds trapped within undisturbed vegetation and on gopher mounds. A newly-formed gopher mound buries existing vegetation, and hence, depending on the timing of disturbance, no seeds are produced on the mound area, or else seeds are buried beneath 5–10 cm of soil. Thus seed production was considered only for undisturbed areas; any seeds falling onto the new surface formed by a gopher mound must come from the surrounding vegetation. Estimates for numbers produced and numbers trapped within undisturbed vegetation were markedly different for some species, notably *Calycadenia, Microseris* and *Orthocarpus*. Predation trials indicated that ants (*Veromessor andrei* Mayr) may have removed significant numbers of seeds of several species, and this is the subject of a further paper (Hobbs 1985). However, predation does not account for the markedly lower number of *Orthocarpus* seeds trapped compared with produced. It is possible that this is due to very localised seed dispersal of this species and the lack of seeding individuals close to seed traps.

Table 1. Frequency of occurrence and mean percentage cover of all species found within 36 50 × 50 quadrats placed randomly within study area in April 1983

	Frequency %	% cover (mean ±1 S.E.)
Agoseris heterophylla (Nutt.) Greene	50	0.7±0.2
Arenaria douglasii Fenzl ex T. & G.	3	0.1±0.1
Astragalus gambellianus Sheldon	17	0.2±0.1
Brodiaea laxa (Benth.) Wats.	47	0.8±0.3
Brodiaea pulchella (Salisb.) Greene	58	1.0±0.3
Brodiaea terrestris Kell	17	0.2±0.2
Bromus mollis L.	50	0.8±0.3
Calycadenia multiglandulosa DC	100	16.0±3.2
Chlorogalum pomeridianum (DC) Kunth.	75	4.5±2.0
Eschscholtzia californica Cham	33	0.5±0.2
Evax sparsiflora (Gray) Jeps.	75	1.3±0.2
Hemizonia luzulifolia DC.	17	0.2±0.1
Lasthenia californica DC. ex Lindley	100	44.6±6.3
Layia platyglossa (F. & M.) Gray	67	1.0±0.4
Lepidium nitidum Nutt.	8	0.1±0.1
Lotus subpinnatus Lag.	50	1.2±0.4
Melica californica Scribn.	5	0.1±0.1
Micropus californicus F. & M.	8	0.2±0.2
Microseris douglasii (DC.) Sch.-Bip.	75	1.7±0.5
Orthocarpus densiflorus Benth.	75	1.9±0.8
Plagiobothrys nothofulvus (Gray) Gray	3	0.1±0.1
Plantago erecta Morris	100	12.9±4.1
Pao scabrella (Thurb.) Benth. ex Vasey	8	0.1±0.1
Sitanion jubatum J.G. Sm.	75	5.4±1.5
Stipa pulchra Hitchc.	43	1.2±0.4
Tillea erecta H. & A.	17	0.2±0.1
Vulpia microstachys (Nutt.) Benth var. *pauciflora* (Beal) Lonard & Gould.	100	7.0±3.1
Bare ground	100	15.0±4.5

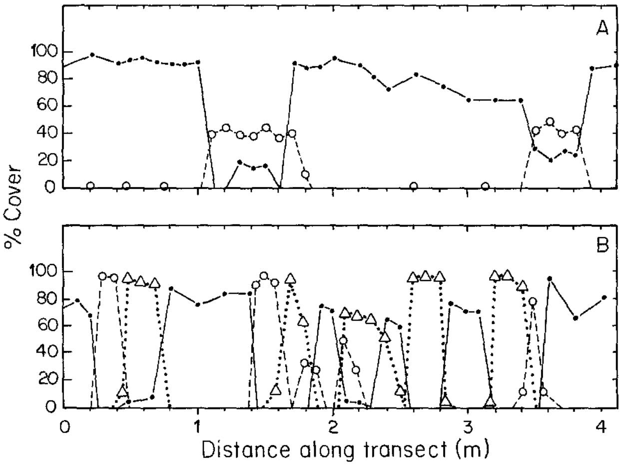

Fig. 1 A, B. Results from two transects 4 m long by 10 cm wide taken within serpentine grassland vegetation: percentage cover of selected species in 10 × 10 cm quadrats demarcated along transects. **A** *Lasthenia californica* (*closed circles*) and *Bromus mollis* (*open circles*). **B** *Lasthenia californica* (*closed circles*), *Stipa pulchra* (*open circles*) and *Sitanion jubatum* (*triangles*)

Table 2. Seed production, seed rain and height of inflorescences on serpentine grassland. Production and inflorescence height estimated in April 1983; seed rain represents total numbers of seeds trapped April–November 1983. Significant differences between undisturbed and gopher mounds, as tested by the Mann-Whitney U test are indicated: * $P<0.05$; ** $P<0.01$

	Estimated seed production (no. m^{-2})	Numbers of seeds trapped m^{-2} (mean ± 1 S.E.: $n=25$)		Mean maximum inflorescence height (cm) ± 1 S.E.: $n=25$
		Undisturbed	Gopher mounds	
Agoseris heterophylla	630	408 ± 90	270 ± 90	16.6 ± 0.6
Bromus mollis	1,730	1,990 ± 600	3,350 ± 540	19.9 ± 0.6
Calycadenia multiglandulosa	12,500	2,310 ± 400	1,180 ± 220*	25.4 ± 0.6
Lasthenia californica	49,200	52,500 ± 3,350	20,600 ± 2,450**	12.2 ± 0.4
Layia platyglossa	290	109 ± 45	54 ± 54	16.5 ± 0.5
Microseris douglasii	1,000	226 ± 90	270 ± 90	15.5 ± 0.5
Orthocarpus densiflorus	14,500	2,210 ± 1,720	360 ± 145	15.3 ± 0.6
Plantago erecta	5,460	3,840 ± 440	1,408 ± 172**	8.5 ± 0.3
Vulpia microstachys Var *pauciflora*	1,200	725 ± 270	1,080 ± 177	22.0 ± 0.8

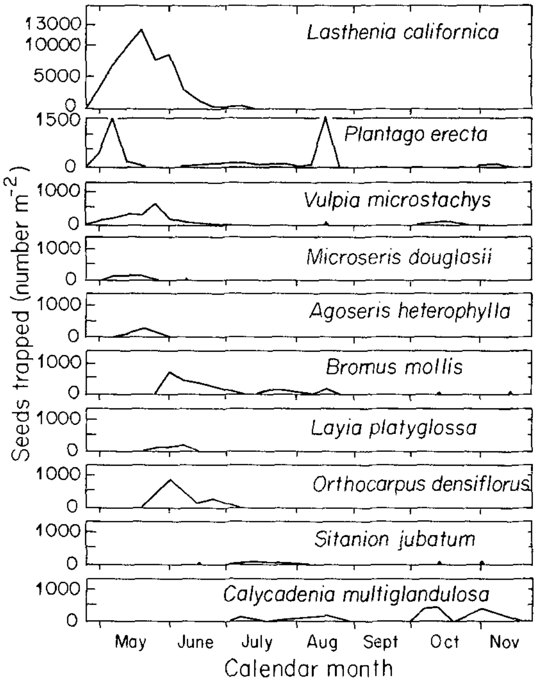

Fig. 2. Seed rain in serpentine grassland: numbers of seeds trapped per week over the period May–November 1983 an estimated from 25 sticky traps (5 cm diameter) in undisturbed vegetation

The seed rain over the period May–November 1983 is illustrated in Fig. 2 as weekly total numbers of seeds trapped. Most species shed their seeds in early summer, corresponding to the time when soil drying and plant death occur, with seed release virtually complete by the end of June. However, *Bromus* continued to release seed throughout the summer and *Vulpia* had a second period of seed release in October. The perennial grass *Sitanion* commenced seed release later, as did *Calycadenia* which continued to release seed into November. *Plantago* had an early peak of seed release followed by a further peak in August. These peaks corresponded to a late spring rain and an unseasonal summer rain respectively. Seed release in this species appears to be partially hydraulic, dried fruits being ejected short distances when wetted. Many fruits were not ripe at the time of the last spring rains and remained intact on the flowering stalks (despite the death of the plant) until the next rain in August. No *Hemizonia* was present in the vicinity of the study site, but in surrounding areas in continued flowering in late summer and did not release its seed until after the first fall rains.

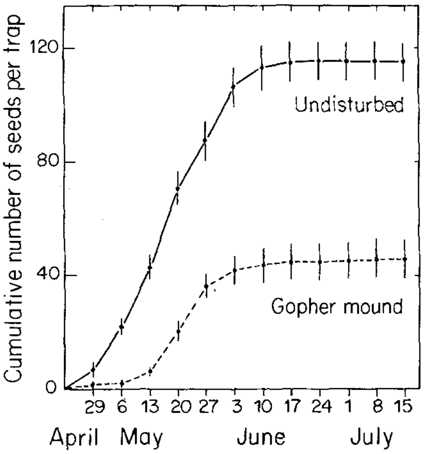

Fig. 3. Cumulative number of seeds of *Lasthenia californica* trapped from April to July 1983 in undisturbed vegetation and on gopher mounds: mean numbers per trap, estimated from 25 traps on each microhabitat. Vertical lines indicate Standard Errors

Seeds of most species were trapped in lower numbers on gopher mounds than in undisturbed vegetation. However, differences were significant only for *Lasthenia, Plantago* and *Calycadenia*, with the seed rain of other species showing considerable spatial heterogeneity. Figure 3 shows the cumulative seed rain for *Lasthenia*, and illustrates the reduction in numbers of seeds reaching gopher mounds compared to adjacent undisturbed vegetation. Thus although sticky traps on gopher mounds were a maximum distance of 25 cm from the surrounding vegetation, far fewer seeds of the dominant species fell within these traps than within traps under closed vegetation. As well as differences in absolute numbers of seeds falling on gopher mounds and undisturbed areas, proportions of the total seed rain contributed by each species also differed. *Lasthenia* made up the greatest proportion of the total rain on both microhabitats (87% in undisturbed; 73% on gopher mounds), but the contribution made by other species,

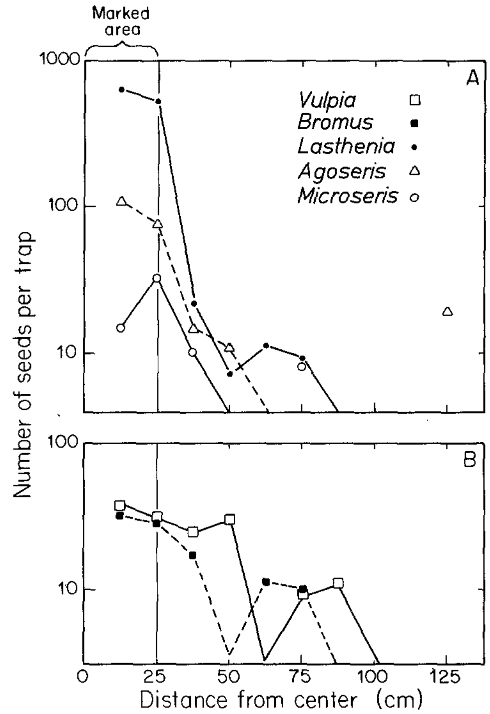

Fig. 4A, B. Numbers of marked seeds trapped at different distances from centre of a circular area (50 cm diameter) where all seeds were marked with red ink: mean of 6 values for each distance. **A** *Lasthenia californica* (*closed circles*), *Microseris douglasii* (*open circles*), *Agoseris heterophylla* (*triangles*). **B** *Bromus mollis* (*closed squares*), *Vulpia microstachys* (*open squares*)

notably *Calycadenia, Bromus, Vulpia* and *Sitanion* increased on gopher mounds.

Seed dispersal

The finding that seeds of several species reached gopher mounds in considerably reduced numbers indicated that dispersal distances were probably rather small. Results from the trial in which we observed dispersal of marked seeds support this idea. Although seeds of all species marked were found 75–125 cm away from the centre of the marked area, the proportions of marked seeds found outside the marked area were generally low. Figure 4 shows the numbers of seeds trapped at each distance from the centre of the marked area, corrected in each case for the difference in area sampled for concentric circles around the marked area. For *Lasthenia, Microseris* and *Agoseris* there was a clear decline in the numbers of seeds trapped with distance from the marked area, with $>90\%$ of the recovered marked seeds being found within the marked area. For *Bromus* and *Vulpia*, on the other hand, the decline with distance from the marked area was less pronounced, with approximately 25% of the marked seeds recovered outside the marked area. A comparison of numbers of marked seeds trapped with an estimate of the total numbers marked indicated a good recapture rate suggesting that the results are reasonably accurate. These findings of limited dispersal are in agreement with studies on other annual plants (e.g. Watkinson 1978; Verkaar et al. 1983), although a more refined study using radioactive tracers could now be implemented to assess less frequent longer distance dispersal, and also dispersal of other species, notably *Plantago.*

Seeds of the three Asteraceae studied here appear to have shorter dispersal distances than the grass species. A reason for this may be found in the relative heights of seed release of the different species. Table 2 gives the mean maximum height attained by inflorescences of the various species at time of seed release, and it is apparent that *Bromus* and *Vulpia* release their seeds on average from several centimetres higher than the other species marked. Sheldon and Burrows (1973) have previously shown that height of seed release can be an important determinant of seed dispersal distance. However, in this case, a secondary factor may be more important. At the time that most annual species released their seed, the abundant *Calycadenia* formed a relatively dense canopy with a mean height of $22.0+0.5$ cm. Most of the seeds released by species such as *Lasthenia* and *Agoseris* were therefore released within this canopy and did not reach the airflow above it. In contrast, seeds released from a position above this canopy could travel several metres. The grass seeds, on the other hand, were released from approximately the top of this canopy and were able to travel further. It is also important to note that seeds of the later flowering species such as *Calycadenia, Hemizonia* and *Sitanion* were all released from greater heights than the early flowering species and hence had the potential to travel further.

Seed storage

Greatly reduced numbers of germinable seeds were detected in soil samples compared with the recorded seed production and rain (Fig. 5), and there were strong seasonal fluctuations in numbers of seeds present in the soil. Numbers of germinable seeds were highest in the late summer and fall, declining during winter and reaching almost zero in spring. Thus, although seeds of most species are shed in May and June, they do not appear in germination tests until later in the summer, indicating a strong dormancy mechanism in all the grassland species to prevent early germination after summer rains. Differences between species are also apparent, however, and most of the seeds germinating from the August samples were of *Bromus mollis*, with the native species not germinating until the October samples.

The virtual absence of germinable seeds during winter and spring indicates that there is very little carryover of seed from one year to the next in this community. This means that virtually all viable seeds produced in the spring germinate in the fall, as has been found in previous studies in California annual grasslands dominated by European grasses (Bartolome 1979; Young et al. 1981).

The numbers of seeds germinating in these samples are relatively low compared with numbers found by Young et al. (1981), and this perhaps reflects the low germinability of many of the native species, as discussed later. Similar reductions in numbers from seed rain to the soil pool have been found by Rabinowitz and Rapp (1980) and Mallik et al. (1984) in other community types. In this study, numbers of seed were generally considerably higher in undisturbed soil compared with in gopher mounds. Most seeds were contained in the immediate surface soil in undisturbed areas, whereas more seeds were found at lower depths in gopher mounds. This was due partially to the soil mixing associated with mound formation and the burial of seeds in the original surface soil under material excavated by gophers. However, seeds dispersing onto gopher mounds may also be more likely to descend to lower levels in the soil

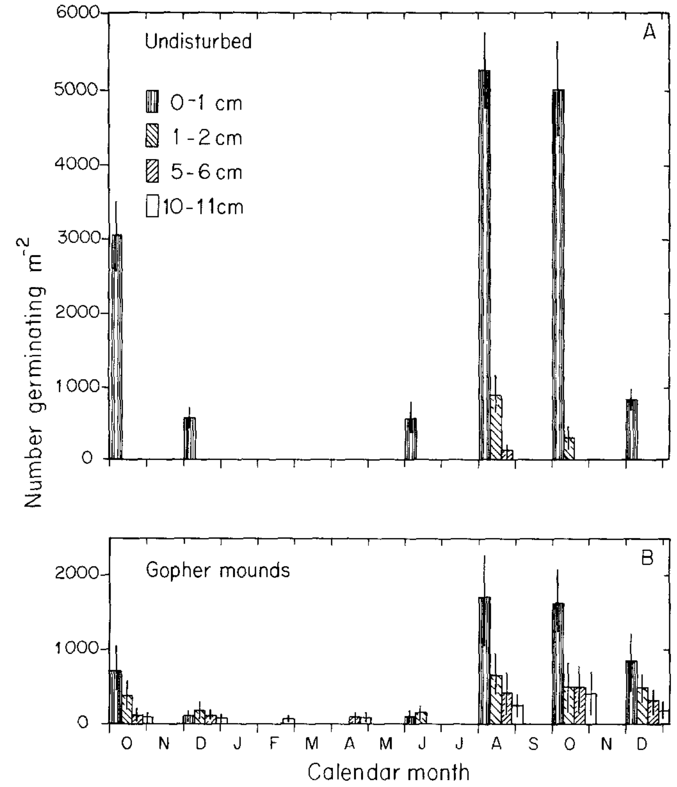

Fig. 5. Numbers of seeds germinating from soil taken from various depths beneath undisturbed areas and gopher mounds at 2 monthly intervals over the period October 1982–December 1983; mean numbers from 25 samples at each depth. Vertical lines indicate Standard Errors

due to the larger soil particle size and less consolidated nature of the mounds. An important feature of the data is that seeds of several species were found at lower soil levels within gopher mounds throughout the year. Thus it is possible that seeds buried by gopher excavations or falling to lower soil levels remain viable longer than seeds near the surface. These seeds may then be important in recolonisation following further disturbance. This may be especially true for species exhibiting strong dormancy, and, for instance, for *Calycadenia* which produces dimorphic seeds, one form of which lacks dispersal structures and has strong dormancy (similar to many other Asteraceae: e.g. Burtt 1977; McEvoy 1984). Stored seed many other Asteraceae: e.g. Burtt 1977; McEvoy 1984). Stored seed may also be important for some of the rarer species present in the grassland – for instance *Arenaria douglasii* and *Plagiobothrys nothofulvus* appeared in permanent plots in 1984 but were absent in 1983. Clearly further study is required of these rarer species and of seeds with strong dormancy.

Germination, survivorship, growth and fecundity

The first significant fall rains in 1983 came at the end of September, and germination was observed in the non-serpentine grasslands within 4–5 days of this rain. However, germination did not occur on the serpentine until after prolonged rainfall on 9–12 November. Figure 6 shows the cumulative numbers of *Lasthenia, Bromus, Plantago* and *Calycadenia* germinating on undisturbed areas and on gopher mounds produced in either April or July. For these and for the other less common species, there was a clear burst

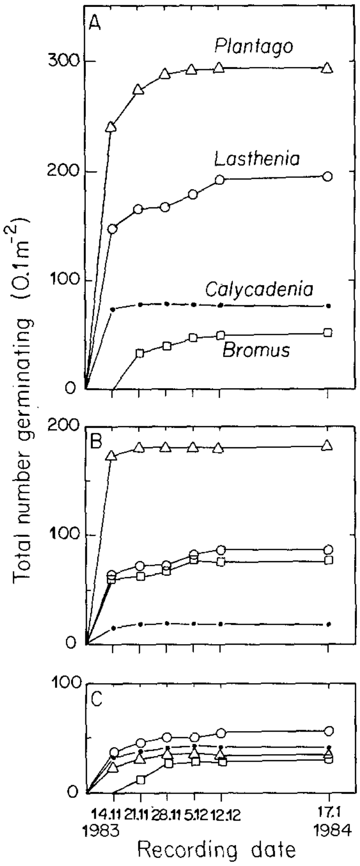

Fig. 6A–C. Cumulative numbers of germinated seedlings observed in 10 10 × 10 cm quadrats over the period November 1983 to January 1984 in each of three microhabitats in serpentine grassland: *Plantago erecta* (*triangles*), *Lasthenia californica* (*open circles*), *Calycadenia multiglandulosa* (*closed circles*), *Bromus mollis* (*squares*). **A** Undisturbed areas. **B** Gopher mounds formed in April 1983. **C** Gopher mounds formed in July 1983

of germination immediately after the heavy rains, with smaller numbers germinating in subsequent weeks. *Plantago* and *Calycadenia* germination was virtually complete by the end of November, while *Lasthenia* and *Bromus* continued to germinate in small numbers throughout December. However, very little further germination of any species occurred subsequently. Very few instances of growth up through gopher mounds of perennials buried earlier were found (cf. Laycock 1958), except for several plants of *Brodiaea* growing back from buried corms. Pratically all recolonisation was therefore from seed near the soil surface.

Table 3 provides a summary of germination, survival, biomass attained and seed set for the 5 most common species found within the permanent quadrats. Other species were too infrequent to produce reliable data. From these data (Table 3a) and Fig. 6 it is clear that there were marked differences in the numbers of seeds germinating between the different microhabitats. Germination of both *Platago* and *Lasthenia* was considerably reduced on gopher mounds, especially those formed in July, but numbers of *Calycadenia* were reduced only on the mounds formed in April. For all species there was an obvious reduction in the numbers of seeds germinating over the numbers estimated to have arrived in the seed rain. This reduction is of a similar order to that found in the soil storage data, and may be attributable to a combination of low viability

Table 3. Results from 10 permanent quadrats (each 10 × 10 cm) set up in undisturbed areas and on gopher mounds formed either in April or July 1983. (mean ± 1 SE). Significant differences between numbers on gopher mounds and on undisturbed areas are indicated (Mann-Whitney *U* test, except for (d), where *t* was used). + increase over undisturbed − decrease: significance levels; * <0.05, ** 0.01, *** 0.001

	Undisturbed	Gopher mounds	
		Formed in April	Formed in July
a) Number of seedlings germinated per m^2 by December 1983			
Bromus mollis	470 ± 90	730 ± 160	430 ± 50
Calycadenia multiglandulosa	700 ± 120	220 ± 40 − −	700 ± 40
Lasthenia californica	1,930 ± 270	890 ± 230 − −	490 ± 210 − − −
Plantago erecta	2,700 ± 190	1,680 ± 350 −	400 ± 120 − − −
Vulpia microstachys	180 ± 30	90 ± 40	230 ± 50
b) Proportion of germinated seedlings which survive to flowering (%)			
Bromus mollis	49 ± 12	90 ± 4	47 ± 11
Calycadenia multiglandulosa	58 ± 10	65 ± 12	100 ± 0
Lasthenia california	58 ± 5	75 ± 7	73 ± 9
Plantago erecta	94 ± 1	82 ± 4	98 ± 2
Vulpia microstachys	87 ± 8	100 ± 0	89 ± 6
c) Number of plants per m^2, April 1984			
Bromus mollis	230 ± 90	680 ± 170 + + +	180 ± 50
Calycadenia multiglandulosa	290 ± 40	160 ± 40 −	420 ± 40 +
Lasthenia californica	1,140 ± 210	590 ± 150 −	390 ± 210 −
Plantago erecta	2,550 ± 180	1,460 ± 350 −	390 ± 120 − − −
Vulpa microstachys	150 ± 30	90 ± 40	200 ± 50
d) Total above-ground biomass per plant (mg) at time of flowering ($n = 10$)			
Bromus mollis	39.6 ± 6.2	71.3 ± 17.4	103.4 ± 24.1 +
Calycadenia multiglandulosa	98.6 ± 32.6	153.3 ± 47.0	701.7 ± 206.0 +
Lasthenia californica	10.2 ± 3.8	14.7 ± 3.5	25.4 ± 3.9 +
Plantago erecta	17.9 ± 4.4	46.7 ± 2.6 + + +	121.8 ± 20.4 + + +
Vulpia microstachys	20.0 ± 4.3	13.7 ± 3.2	36.4 ± 4.5 +
e) Number of seeds produced per plant			
Bromus mollis	9.9 ± 1.1	13.1 ± 0.9 +	19.4 ± 3.2 + +
Calycadenia multiglandulosa	17.9 ± 2.8	29.1 ± 5.3	37.1 ± 3.8 + + +
Lasthenia californica	20.3 ± 1.7	31.2 ± 3.6 + +	21.8 ± 3.8 + +
Plantago erecta	3.7 ± 0.1	6.9 ± 0.4 + + +	7.4 ± 0.6 + + +
Vulpia microstachys	9.3 ± 1.7	19.4 ± 2.3 + +	20.0 ± 4.3 +

Table 4. Comparison of germination success in laboratory (6 month old seeds treated with 0.01% gibberellic acid in deionised water) with estimated proportion of total seed rain which germinated in marked field plots (mean ± 1 SE, $n = 10$)

	% germination in lab	% of total seed rain germinated in field plots
Agoseris heterophylla	35 ± 8	7 ± 5
Bromus mollis	100 ± 0	24 ± 5
Calycadenia multiglandulosa	30 ± 8	30 ± 5
Layia platyglossa	45 ± 5	0 ± 0
Lasthenia californica	5 ± 1	4 ± 1
Microseris douglasii	15 ± 5	0 ± 0
Orthocarpus densiflorus	0 ± 0	1 ± 1
Plantago erecta	100 ± 0	70 ± 3
Vulpia microstachys	15 ± 2	25 ± 4

and seed predation. Table 4 gives the germinability of the main annual species, as tested in the laboratory, compared with that estimated from the field analyses. *Lasthenia* and *Orthocarpus* (the species with the smallest seeds) had very low germination rates both in the lab and in the field. Lab and field germination rates match fairly well for *Calycadenia* and *Vulpia*, but field rates were considerably lower for *Agoseris, Bromus, Layia, Microseris* and *Plantago.* We argue in another paper that predation by harvester ants may reduce numbers of seeds of all these species except *Bromus* (Hobbs 1985). Gulmon (1979) found a similar relationship between numbers of *Bromus* seeds available and germinating (30%) on a non-serpentine substrate, but the causes of this reduction have not been investigated.

Differences between microhabitats in number of seeds germinating can to some extent be explained by the differences in seed input discussed previously; the three species with reduced germination on gopher mounds also had significantly lower numbers of seeds falling onto the mounds. Although data on seed rain are available only for mounds formed in April before seed fall started, it is clear from Fig. 2 that the mounds formed in July would receive far fewer seeds of most species since the bulk of seed fall had occurred in May–June. These mounds would be colonised only be species which were still dispersing seeds later in the summer; this includes *Bromus, Vulpia, Calycadenia* and the perennial grasses, all of which have relatively tall inflo-

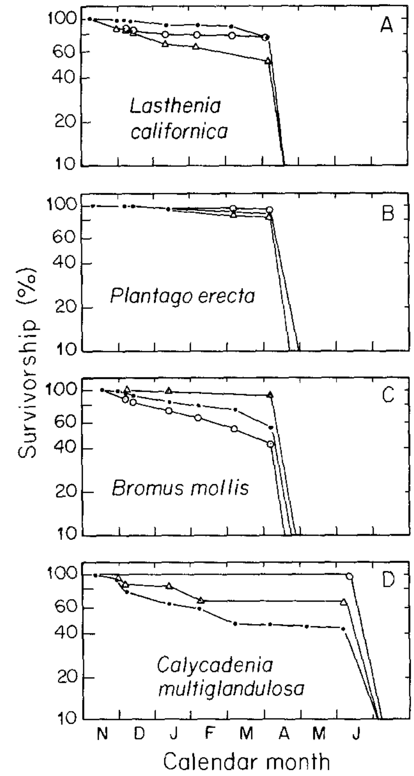

Fig. 7A–D. Survivorship curves for annual species on three microhabitats within serpentine grassland, from germination in November 1983 to flowering in spring 1984 (expressed as proportion of initial number of seedlings which remain alive at each recording): undisturbed areas (*closed circles*), gopher mounds formed in April 1983 (*triangles*), gopher mounds formed in July 1983 (*open circles*). **A** *Lasthenia california*. **B** *Plantago erecta*. **C** *Bromus mollis*. **D** *Calycadenia multiglandulosa*

rescences which enable dispersal onto mounds. *Plantago* also released seeds later in the season, and was thus able to colonise mounds formed in July, but in reduced numbers. The marked reduction in numbers of seedlings found on mounds formed in July may be due to differential germination rather than differences in seed input.

Survivorship of germinated seedlings to flowering is given in Table 3b and survivorship curves are shown in Fig. 7. Survivorship clearly varied between species and microhabitats. *Plantago* and *Vulpia* showed consistently high survivorship rates on all three substrates. *Lasthenia* had a slightly higher survivorship on gopher mounds than in undisturbed vegetation, while *Calycadenia* showed a dramatic increase in survivorship on mounds formed in July. *Bromus*, on the other hand, had a higher rate of survival on mounds formed in April. All species showed typical Deevey Type I curves with the rate of mortality increasing after flowering and seed set. Such patterns have been reported previously in other annual communities (e.g. Schaal and Leverich 1982). *Bromus, Lasthenia, Vulpia* and *Plantago* showed fairly constant low mortality rates over the growing season, but for *Calycadenia* mortality was highest in the period December to February, with no subsequent mortality until after flowering in the summer. This indicates perhaps a greater susceptibility of *Calycadenia* to competition from other species in the early stages of growth; this comes from *Plantago* and/or *Lasthenia* in undisturbed vegetation and *Bromus* on mounds formed in April. Further evidence for this hypothesis comes from observations that *Calycadenia* disappears when grass growth is stimulated by the addition of fertiliser (Gulmon and Hobbs, unpublished).

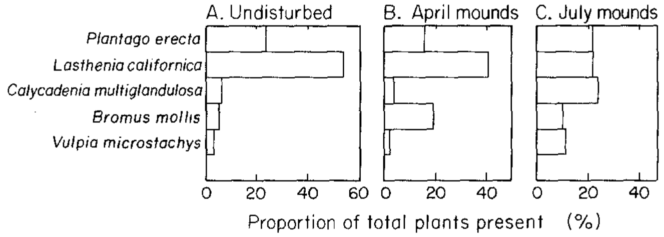

Fig. 8A–C. Relative abundances (% of total number of plants present) of major annual species on three microhabitats on serpentine grassland in April 1984. **A** Undisturbed areas. **B** Gopher mounds formed in April 1983. **C** Gopher mounds formed in July 1983

The relative scarcity of seedlings establishing after the initial burst of germination makes it difficult to analyse survivorship in relation to establishment time. However, it is clear for all the species studied that mortality was higher in seedlings establishing later in the year. Individuals of *Lasthenia* and *Bromus* germinating in December commonly did not survive until the next recording. Thus most of the plants surviving to flowering were those that germinated in the initial cohort.

Differences in number of seeds available and subsequent survival of germinated seedlings on the different microhabitats led to the presence of different numbers of adult plants of the major species (Table 3c). Thus for mounds formed in April, numbers of *Calycadenia, Lasthenia* and *Plantago* were reduced, but numbers of *Bromus* were higher. On mounds formed in July, numbers of *Lasthenia* and *Plantago* were again reduced, but *Calycadenia* was more abundant. Increased numbers of *Bromus* on April mounds and *Calycadenia* on July mounds were both due primarily to increased survival on these particular microhabitats.

These differences led to quite different relative importances of the main species on the three different microhabitats (Fig. 8). In undisturbed areas, *Plantago* and *Lasthenia* were dominant, with other species present in relatively small numbers. On gopher mounds formed in April, *Lasthenia* and *Plantago* were still abundant, but *Bromus* became relatively more important, while on mounds formed in July, dominance was no longer concentrated in *Lasthenia* and *Plantago*. Rather there was a much more even community composition with an increased importance of *Calycadenia*.

So far only plant numbers have been considered. However, field observations indicated that performance of individual plants also varied between microhabitats in terms of both overall growth and seed production. Data obtained from harvesting supported this (Table 3d, e), with all species showing significantly greater biomass on mounds formed in July (and also in April for *Plantago*). This was matched by significant increases in seed production for all species, although higher biomass was not always related to increased seed production on the same microhabitat (e.g. *Vulpia* on April mounds and *Lasthenia* on July mounds). Singer and Ehrlich (1979) have also pointed out a potentially important result of increased plant size of *Plantago* on open gopher mounds – these larger, open-grown plants may survive several weeks longer before senescence at the onset of the dry season and may allow larvae of *Euphrydryas editha*, which use *Plantago* as their food plant, to complete their development.

Improved growth and reproduction on gopher mounds may indicate reduced competition on these more open microhabitats, or simply greater resource availability. Certainly, a gopher mound represents the addition of 5–10 cm depth of soil on top of the existing surface, providing greater rooting depth. This may explain why the more deeply-root species such as *Calycadenia* perform better on gopher mounds. Although *Hemizonia* was not common in the study area, we have observed that it behaves in a similar manner, growing much larger on open gopher mounds than in undisturbed vegetation; Gulmon et al. (1983) have already noted that this deep-rooted species grows mainly in deeper soil. Greater resource availability may also account for the greater success of *Bromus* on mounds formed in April. Since this species is an invader of the serpentine, it may require slightly elevated nutrient levels to perform adequately. Trials have indicated that its performance is greatly improved with added fertiliser (Turitzen 1981; Gulmon and Hobbs unpublished). Its lower survival rates on mounds formed in July may be due to increased water deficits on the more open habitats which we have found to dry out more quickly (Hobbs unpublished).

Conclusion

This study has viewed the spatial and temporal dynamics of an annual grassland community on serpentine soil by examining the population dynamics of the main annual species present in relation to disturbance caused by gophers. The results have indicated that gophers exert a strong influence on the dynamics of the community through the continual tilling of the soil and production of bare soil microhabitats. Spatial patterning within the community is strongly influenced by differential colonisation of gopher mounds and subsequent differences in survival of the annual species present. Although there is not a clear guild of 'fugitive' species found only on gopher mounds, for instance as described for badger disturbances by Platt (1975), species abundances do vary greatly between undisturbed areas and gopher mounds formed at different times of year. There are, in addition, distinct differences between gopher mounds formed at different times of year which can be explained almost entirely by comparing the timing of mound formation with that of seefall of the grassland species. The longer lived species (i.e. *Calycadenia* and perennial grasses) release their seeds later in the year, and are thus able to colonise gopher mounds formed late in summer which are 'unavailable' to the shorter-lived species. This may then allow these species to establish in the absence of competition from the species which dominate in the undisturbed grassland. The data here suggest that is the case for *Calycadenia* and it may also be true the other longer-lived species. Certainly, Bartolome (1981) has shown that *Stipa pulchra* is unable to compete with annual grasses, and he suggested that *Stipa* requires disturbance for establishment. Patterns such as those shown in Fig. 1 may then be the result of colonisation by the perennial grasses of a set of gopher mounds formed late in the season. Clearly, more detailed studies of competition at the seedling stages between long- and short-lived species are required to test this hypothesis. We can hypothesise therefore that some of the species present, including the perennial species, may require the presence of gopher disturbance to enable them to establish and remain within the community. This would be in contrast to the prediction by Tilman (1983) that gopher activity should maintain annuals in the community by preferential feeding on perennial species. On Jasper, Ridge gopher activity would maintain the presence of perennials within an otherwise annual-dominated system. Gopher activity would, nevertheless, maintain a higher overall diversity, as would be predicted by recent hypotheses on the maintenance of community diversity (e.g. Grubb 1977; Huston 1979).

This study was conducted over a single annual cycle. The results found may vary with year to year environmental fluctuations. Timing of climatic events with consequent effects on germination, growth and phenology of the plant species present may vary greatly from year to year. For instance, a period with no rain after the initial germination event in the fall may lead to greater seedling mortality than was found here, and may not affect all microhabitats equally. Similarly, the timing of rains in the spring may lead to more rapid soil drying and seed dispersal by the short-lived annuals. This was, in fact, the case in spring 1984, when seed dispersal began several weeks earlier than in 1983. This may have an effect on the distances seeds are dispersed, since in 1984 seed heads of many species were above the canopy of *Calycadenia* which was still at an earlier stage of growth than in 1983. Bartolome (1979) has also pointed out that the small proportion of seeds retained in the soil store may play an important role in recovery after extreme drought years when little fresh seed is produced. From this point of view, and in more general terms, the return-time of gopher activity is very important; i.e. the time between one excavation and the next at any particular position may also have an important effect on community composition. At a longer time scale, fluctuations in the numbers of gophers present in the area may also have pronounced effects on the plant community by altering the amount and frequency of disturbance.

Clearly, therefore, longer-term studies of the dynamics of the grassland community are required, and these are at present underway with permanent plots in areas open to, and excluded from, gopher activity. However, this short-term study has emphasised the importance of gophers in shaping the dynamics of the plant community. It has also demonstrated that plant population dynamics must be studied in space as well as time.

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