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GERMINATION AND SEEDLING ESTABLISHMENT IN CALIFORNIA ANNUAL GRASSLAND

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SUMMARY

(1) Data for plant density, germinable seed in the soil, and seed production in annual grassland were obtained at Hopland Field Station, California, U.S.A., in 1973 and 1974. The study combined indirect estimates of numbers of seed in the soil, germination in soil samples containing natural seed, and estimation of plant density.

(2) Autumn patterns of establishment differed significantly between the two study years. Plant density increased through the autumn, reaching peaks of 261·8 and 345·3 plants per dm^2 in the seventh week after germination began, in 1973 and 1974 respectively.

(3) The numbers of germinable seed in the top 6·4 cm of the soil prior to the start of the growing season were 670·5 per dm^2 in 1973 and 610·2 per dm^2 in 1974, and thus showed little difference between years.

(4) Comparison of depletion of the seed-bank in the soil and increase of plant density showed that seeds germinating in the first week of the growing season produced fewer established seedlings than seeds germinating in the second or third weeks. The few seeds remaining in the fifth and sixth weeks had a high probability for successful establishment.

(5) Six species-groups exhibiting contrasting strategies for germination and establishment are discussed in detail.

INTRODUCTION

Vegetation composed of annuals affords special opportunities for the investigation of dynamic aspects of plant populations. Plant responses to induced and natural environmental variation show up rapidly, because germination, establishment, seed production and death occur in each growing season. Equilibrium of species-composition, rather than developing over decades as with vegetation composed of longer-lived plants, may be reached within a single growing season. Early patterns of establishment by several important annual plant groups determine the overall yearly and seasonal changes in vegetation, because survival of seedlings in the early part of the growing season permits them to live through the rest of the growth year.

The Californian annual grassland extends over an area of approximately 10-million ha, both as open grassland and as understorey in oak savannah and chaparral. Recent reviews by Heady (1977) and Heady *et al.* (1977) describe the major regions of annual grassland in California.

California grassland vegetation is largely annual. Many introduced species are shared with other parts of the world having a mediterranean climate. The vegetation is quite different from that present before the introduction of alien plants and animals, beginning in the 18th century. Although nearly all native plant species have survived, introduced annuals dominate in density and cover. At the Hopland Field Station, the location of this study, introduced plants comprise between 80 and 97% of the foliar cover (Heady 1956), a typical degree of dominance by aliens over the native plants.

Mediterranean annual species exhibit a characteristic growth pattern, which may be divided into five stages: (1) autumn germination of seeds mostly produced at the end of the previous growing season; (2) seedling establishment; (3) slow vegetative growth through the autumn and winter; (4) flowering and seed production, followed by senescence and death of plants; and (5) summer carry-over of seed (Bartolome 1976b). Although these five stages are repeated yearly, composition, phenology, and productivity of the vegetation vary considerably (Evans, Kay & Young 1975; Pitt 1975).

The general pattern of germination and establishment is well-known for Californian annuals. Germination starts following the first autumn rains of 15–25 mm, with a greening of the aspect of the vegetation within a few days. Species respond differently, however, and the detailed pattern of germination and plant establishment has been reported only briefly (Bartolome 1976a). Questions to be considered in the present study include:

(1) how do autumn population densities differ between years?

(2) how do autumn population parameters differ within years, and do these changes show different patterns between years?

(3) what is the relationship between available seed in the soil and plant establishment?

THE STUDY SITE

The study was conducted at the Hopland Field Station of the University of California in north-western California (39°N, 123°W), from the autumn of 1973 to the spring of 1975. Approximately 60% of the vegetation of the 2000-ha station is grassland and woodland with grass. The climate is mediterranean, with cool wet winters and hot dry summers. Rainfall averages *c.* 980 mm per year, with substantial fluctuations about the mean; it amounted to 1438 mm in 1973–74 and 890 mm in 1974–75.

The study site has been used for experimental work on annual vegetation since 1952, and a 40 × 40 m exclosure was constructed in 1958 to eliminate sheep-grazing. The exclosure itself has long consisted of open grassland, although scattered oak trees (*Quercus* spp.) are present nearby. The soil is a fine sandy loam, 0·6–1·0 m deep, with rapid surface drainage. The slope is about 10%, with a south-east aspect.

This study continued experimental treatments established in 1967 to investigate the effects of removal of varying quantities of natural mulch at the end of each summer. Mulch-treatment levels in a 5 × 5 latin square aimed to retain 0, 280, 560, 840 and 1120 kg ha^{-1} oven-dry weight on the ground at the start of the autumn season. A more detailed description of the method is given elsewhere (Bartolome 1976b).

METHODS

Plant density was estimated by removal of five 2·5 × 2·5-cm squares of soil with rooted plants per treatment, seven times at weekly intervals, beginning in the first week following significant germination. The blocks of soil and plants were placed in plastic bags and live plants identified and recorded in the laboratory. The growing season for the annuals started on 11 October in 1973 and on 31 October in 1974. In this paper, sample dates do not refer to calendar dates, but to weeks from the start of the growing season.

Reserves of seed in the soil were estimated from soil cores 4·1 cm in diameter and 6·4 cm deep. Two samples per treatment were taken, monthly in 1973 and weekly in 1974, beginning before the first rains. Samples were air-dried for 2 weeks, crumbled by hand, placed on vermiculite in plastic cups, covered with a thin layer of sand, and watered daily with tapwater and weekly with 0·1-strength Hoagland's solution. As seedlings appeared they were identified and discarded. Half of the samples from the autumn of 1974 were transported directly to the glasshouse, where growing plants were removed, and watering commenced immediately.

Seeds per plant were counted on a random sample of individuals in late April of 1974, and seed production per unit area was estimated from plant density at the same time. Seed-production estimates at the end of the 1974–75 growing season involved actual counts of seed judged from each 2·5 × 2·5-cm sample obtained for plant-density determinations. Counts for *Erodium* spp. in both years and *Taeniatherum asperum* Nevski. in 1975 were made in a 30 × 30-cm plot.

In the final analysis, the species were grouped into five categories illustrating differing strategies of establishment. Over fifty species appeared in at least one sample, but most did not reach levels of abundance sufficient to show statistical significance. A sixth category, 'total plants', shows the overall pattern of change in the plant population.

The first species-group, *Festuca* spp., consisted of about 95% *Festuca bromoides* L. (syn. *Festuca dertonensis* (All.) Asch. & Graebn.), and included several other species within the subgenus *Vulpia*, such as *Festuca myuros* L. and *F. microstachys* (Nutt.) Benth., which were not vegetatively recognizable as separate entities. *Festuca* spp. formed nearly 50% of the plants at the study site. *Aira caryophyllea* L., in the second species-group, displayed an unusual pattern of establishment, and was also an important component of the vegetation. *Taeniatherum asperum* illustrated a third distinctive pattern of germination. Legumes, the fourth species-group, comprised six species of *Trifolium*, *Lotus micranthus* Benth., and several *Lupinus* spp. This important group incorporates plants with hard seeds. *Erodium* spp., the fifth species-group, consisted predominantly of *Erodium botrys* (Cav.) Bertol., with a small component (5%) of *Erodium obtusiplicatum* (Maire, Weiller and Wilcz.) J. T. Howell. This group exhibited yet another distinctive reproductive strategy.

AUTUMN PATTERNS OF SPECIES-POPULATION CHANGE

Establishment in 1973, following rains in early October, was slow, with two 1-week-periods lacking significant germination interspersed with significant jumps in numbers of new plants (Fig. 1). Germination in the autumn of 1974 began 3 weeks later than in 1973. Near-maximum seedling densities for several species were attained before the second week of the 1974 autumn growing season. This greater plant density attained in the autumn of 1974 was maintained through the winter, to give substantially more plants in spring 1975 than in spring 1974.

The dramatic differences in plant numbers between the two years of the study were generally not accompanied by a similar change in the bank of germinable seed in the soil. Although total plant numbers increased significantly from 1973 to 1974, the estimated

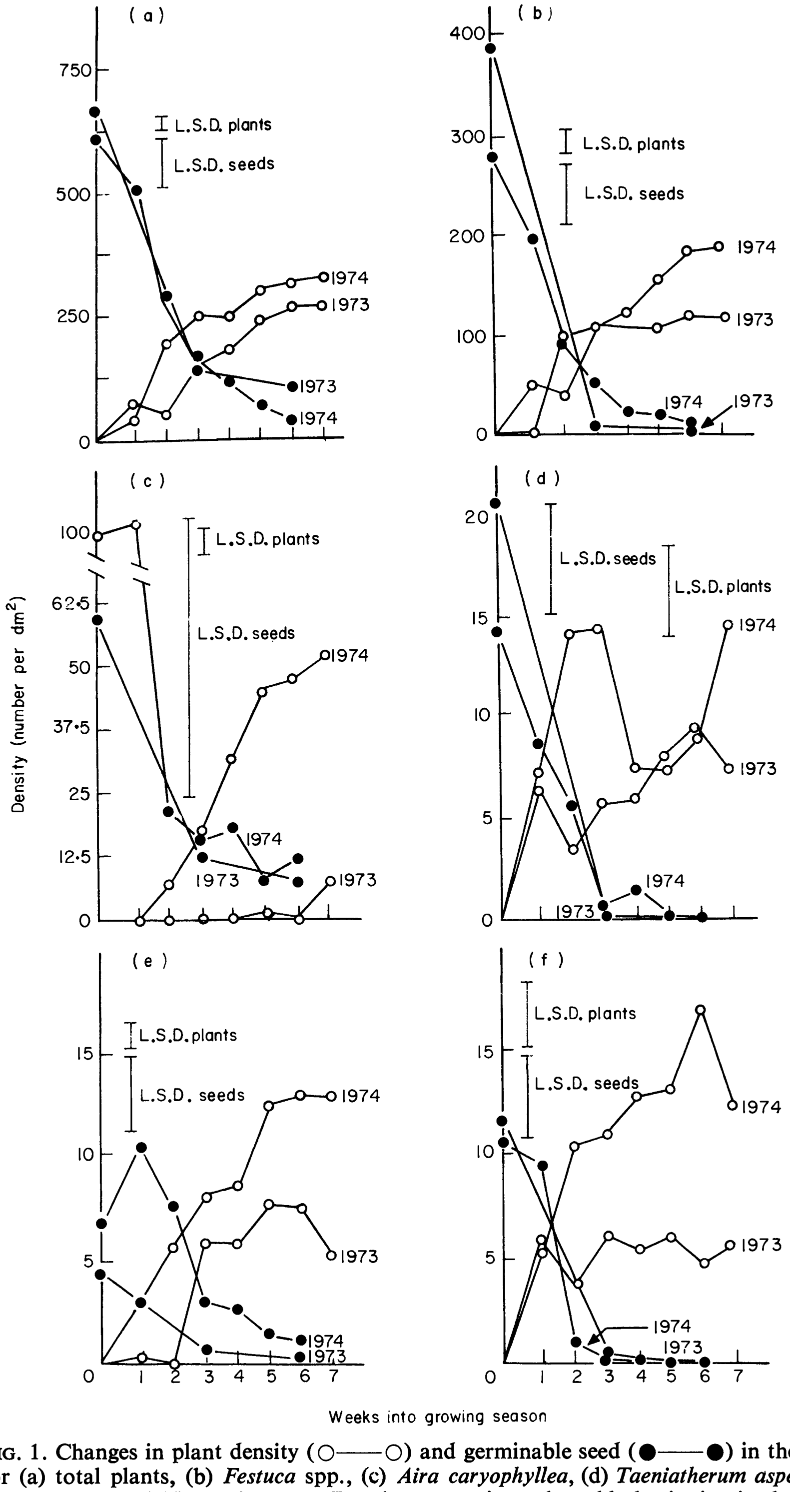

FIG. 1. Changes in plant density (○——○) and germinable seed (●——●) in the soil for (a) total plants, (b) *Festuca* spp., (c) *Aira caryophyllea*, (d) *Taeniatherum asperum*, (e) Legumes, and (d) *Erodium* spp. Density was estimated weekly beginning in the first week following rainfall sufficient to start germination. The first soil sample was collected in late summer before the autumn rains. Least significant difference (L.S.D.) between means is defined for $P < 0{\cdot}05$.

seed reserves in the upper 6·4 cm of soil prior to the start of the growing season declined from 670·5 dm^{-2} to 610·2 dm^{-2}. Because so few of the total seeds produced one year become established the following year, small differences in total seed are unlikely to have a strong influence on total plant numbers.

The plant population of autumn 1974 was established with a pattern of rapid initial germination, but only 35% of the seeds which germinated in the first week produced established seedlings. In the second week, with the largest increase in plant numbers, the numerical increase in seedlings was 70% of the decline in seed numbers. The apparent percentages of seeds successfully establishing seedlings in the third, fourth, fifth and sixth weeks were 40, 0, 87 and 74% respectively. Success rates underestimate the true rates except for the first week, because the increase in plant density does not allow for mortality of previously-established seedlings.

The *Festuca* species-group was the most abundant in the study area. It produced large quantities of seed (Table 1) which germinated throughout the autumn. This pattern of prolonged germination was particularly pronounced in 1973 (Fig. 1). Once established and several weeks-old, the seedlings of *Festuca* spp. suffered little mortality through the winter and spring. Seed of *Festuca* had a high percentage germination at the beginning of the growing season, but significant numbers were still present in the soil in April (Table 2). Seeds still viable in the soil during winter and spring would not have been numerous enough to affect the established plant population, and thus constituted an unimportant component of the *Festuca* population under the conditions observed, despite statistical significance.

TABLE 1. Estimated seed production in four groups of plants, expressed as seeds per dm^2 and mean number of seeds per plant, in spring 1974 and 1975

Plant group	Seeds per dm^2 Spring 1974	Seeds per dm^2 Spring 1975	Seeds per plant Spring 1974	Seeds per plant Spring 1975
Festuca spp.	1227·6	438·6	10·0	3·6
Aira caryophyllea	Not sampled	364·6	Not sampled	6·8
Taeniatherum asperum	Not sampled	14·0	Not sampled	Not sampled
Erodium spp.	12·4	18·6	2·4	1·4

Aira caryophyllea did not begin to germinate until several weeks into the 1973 growing season and one week into the 1974 season (Fig. 1). In contrast to *Festuca* spp. and most of the rest of the plant population, maximum *Aira* numbers were not reached until mid-winter. Where site conditions are favourable for *Aira*, available seed may limit numbers. *Aira* increased markedly in density from the first to second year. The estimated density of seed in the upper 6·4 cm of soil in the autumn of 1973 was 58·7 dm^{-2}, and in the autumn of 1974, 98·7 dm^{-2}. Seed-production data from spring 1975 of 364·2 seeds dm^{-2} (Table 1) suggest a continued increase in *Aira* on the plot. *Aira* seeds disappeared rapidly in the 1973 season, with little apparent establishment until late in the autumn. The pattern of establishment in 1974, perhaps due to the later onset of rains, showed a short delay in germination but a higher establishment rate. The lack of weekly data for seed numbers in the soil precludes more detailed discussion of the 1973 season.

In 1974 *Aira caryophyllea* showed a peak in the numbers of germinable seed in the soil in the first week of the season (Fig. 1), but no germination until the second week, when

TABLE 2. The numbers of seeds germinating per dm^2 in soil samples collected in spring 1974 and placed under favourable conditions in a glasshouse (a) within 2 weeks of collection, (b) after storage in the laboratory for 10 months; * = difference between treatments significant at $P < 0.05$ by *t*-test

	Sample collected 16 Feb. 74		Sample collected 2 Apr. 74	
	Germination trial begun			
Plant group	(a) 14 Mar. 74	(b) 16 Dec. 74	(a) 19 Apr. 74	(b) 16 Dec. 74
Festuca spp.	0	5·1*	0	4·8
Aira caryophyllea	0·3	8·7*	0	8·7*
Taeniatherum asperum	0	0	0	0
Legumes	0	0	0	0·6
Erodium spp.	0	0	0	0·3
Total plants	26·3	59·0*	15·5	70·7*

the reserves in the soil dropped spectacularly and a few *Aira* plants became established. Unlike other species, after that initial rather unsuccessful crop *Aira* steadily established from seeds present in the soil, with little apparent mortality. *Aira* was able to accomplish this late establishment best on plots without any mulch. Germination trials indicated the presence of viable seeds in the soil in spring (Table 2). These could germinate during the spring but could alternatively carry over to another year. *Aira* was most abundant on sites with least mulch (Bartolome 1976b). A pattern of increase would begin with an invasion of bare ground, with density during the first year limited probably by the amount of residual seed from past years. Then, if low mulch were maintained, *Aira* would maintain itself at a high density, as individual plants produced an abundance of seed.

The number of germinable seeds in the soil does not account for observed changes in the autumn seedling-density of *Taeniatherum asperum* (Fig. 1). Germination trials showed small quantities of seed in the soil after the third week. Since *Taeniatherum* was observed to germinate in the autumn, winter and spring, and apparently viable caryopses were present in spring soil-cores, seed dormancy is indicated. A variety of seed treatments failed to promote germination of *Taeniatherum* at any time other than in late summer and early autumn (Table 2). *Taeniatherum* thus appears to show yet another contrasting pattern of establishment. The seedlings which appeared to be firmly established died late in the autumn, with the elimination of *c.* 50% of the crop. Other grass species suffered mortality during the germination process; *Taeniatherum*, however, died later when the seedlings were several weeks old. Genetic variation within the population of *Taeniatherum*, as reported by McKell, Robinson & Major (1962), may be important.

Legume numbers increased throughout the autumn of 1974 as seed numbers declined (Fig. 1), following an initial increase in the number of germinable seeds in the soil between the samples taken before the start of the growing season and those from the first week of the growing season. However, increases in legume seedlings after the fourth week of the season were not accompanied by corresponding decreases in germinable seed content of the soil. In both years plant density increased in a similar pattern, yet attained levels higher than the apparent number of seeds in the soil. Germination of viable seeds present in the soil from previous years is not indicated, since very few legume seeds could be germinated in February and April under the treatments applied (Table 2). Dormancy is a well-documented factor in legumes, and the glasshouse germination method did not produce consistent results. Many dormant legume seeds apparently would germinate in the field but not in the glasshouse.

Erodium showed a conservative reproductive strategy. Although seeds were produced in excess of those germinating the following season, a large proportion of *Erodium* seeds produced established plants. *Erodium* showed almost immediate and synchronous germination with the first substantial rains in autumn. Samples taken after the second week of the 1974 season did not reveal sufficient *Erodium* seed in the soil to account for increases in plant density. The initial increase in plant density observed in the first 1974 sample also was not accompanied by a comparable drop in the seed reserves in the soil. *Erodium*, although an important component of the vegetation in terms of foliar cover and biomass early in the season, is present at a low density. Thus the accounting discrepancies in estimates of soil-seed depletion for *Erodium* may be due to sampling error and the techniques used in this study. *Erodium* displayed population patterns consistent with what might be expected from the characteristics of the plant. An *Erodium* seed is large, with a highly specialized dispersal system, and germinates quickly. The young plant has a fast-growing, extensive root system, and the vigorous seedling forms a winter rosette (McCown & Williams 1968). These qualities suggest a species which has evolved a strategy that ensures the survival and maturation of individuals rather than a strategy of over-production and heavy mortality, but enough survival to ensure perpetuation of the species. *Erodium* contrasts particularly with *Aira caryophyllea* in these respects. It is widely-distributed in the Californian grassland (Janes 1969), and little affected by mulch treatment (Heady 1956; Bartolome 1976b). *Erodium* numbers appeared stable on the study plot, though there were moderate increases observed from 1973–74 to 1974–75.

DISCUSSION

The approach adopted in the experiments presented here has not previously been much applied to the grasslands of the United States. The results cover a single area of the Californian annual grassland and a limited period of time. No attempt was made to evaluate genetic variation within populations. However, the methodology has a wide application and much potential for extension.

The present study has shown that important processes influencing botanical composition and plant density in the Californian annual grassland occur during the period of seed germination and seedling establishment. Previous attempts to explain botanical composition omitted data from this period, when floristic composition is determined, i.e. the first weeks of the growing season (e.g. Heady 1958; Pitt 1975). The changeover from disseminules to autotrophic plants is likely to be critical in many other vegetation types. Studies attempting to relate vegetation change to physiological and competitive capabilities of mature plants may need to be re-evaluated because patterns in plant succession are more likely to be determined at the times of germination and establishment than later in the life cycle.

Patterns of change in the total density of seeds and plants serve to identify a vital point, implied by Major & Pyott (1966). In annual grassland many species are represented as a neglected living part of the system, dormant seed. At a given time, a species may be present as (1) seed in inflorescences, (2) seed in the soil in a state of primary dormancy, (3) viable seed ready to germinate but not yet stimulated to do so by autumn rains,

(4) seedlings still dependent upon reserves stored in the seed endosperm, or (5) as mature plants.

Those plant groups described illustrate different patterns of plant establishment and depletion of soil-seed reserves. The grasses *Taeniatherum asperum* and *Aira caryophyllea* and the forbs *Erodium* spp. respond differently. The reproductively conservative *Taeniatherum* produces relatively few seeds, with apparently complex dormancy patterns; seed production is relatively uniform from year to year. *Aira*, in contrast, is reproductively plastic; it apparently survives and produces seed better with few competing seedlings of other species, perhaps due to a slow rate of germination. *Aira* plants on favourable sites in 1974 produced copious quantities of seed, which in the following year resulted in greatly increased *Aira* density. *Erodium* spp. are reproductively conservative in terms of seeds produced and seedlings established. Yet these species germinate very early in the season, within the first few days following rain. Thus *Erodium* numbers may be reduced substantially if rains come early and are followed by severe drought stress.

Seed-reserve data reported in this study do not precisely reflect the total quantity of seed available in the soil, because seeds were not directly counted. Of particular interest would be the role of viable seed carried over from past years. Such a reserve substantially affects long-term persistence of a species in the vegetation. Quantification of reserves needs more work, yet indications are that many of the species discussed probably have a small carry-over of viable seed from year to year. This carry-over is unimportant to the total population in most years because carried-over seeds are a small proportion of the current crop. However, in a really severe drought during the growing season, continued local survival of a species would be assured by buried, viable, dormant seed.

This paper has focused attention on several aspects of the Californian annual grassland. Clarification of these aspects should aid both understanding of processes and management. The micro-environment in the first few days of the season needs critical study. Effects of selective processes during the dormant seed stage and the very early seedling stage need experimental testing. Relations of dormant and germinating seeds to their environment should yield meaningful information applicable to the whole vegetation. The type of study performed here thus needs to be extended to other annual-grass locations.

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