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COMPETITION FOR NUTRIENTS AND LIGHT BETWEEN THE ANNUAL GRASSLAND SPECIES *BROMUS MOLLIS* AND *ERODIUM BOTRYS*

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Abstract. Experiments showed that when competition between the common grass resident, *Bromus mollis,* and an associated forb, *Erodium botrys,* was primarily for sulfur and crowding was not intense, *Erodium* growth was much greater than in pure stands, and *Bromus* growth was markedly less. With competition under a low sulfur regime, *Erodium* acquired a disproportionate share of the available sulfur because of its more rapid root extension. At high sulfur levels, *Bromus* became increasingly competitive as its population density was increased, and wide ratios of *Bromus* to *Erodium* virtually eliminated *Erodium.* Leaf area and illumination profiles revealed that *Bromus* became the superior competitor for light because of its greater stature and more erect leaf habit when exposed to favorable nutrition and population density, and that *Erodium* supremacy at low sulfur levels and sparse population densities was closely associated with reduced leaf-area production by *Bromus.*

INTRODUCTION

Bromus mollis and *Erodium botrys* are among the most abundant species in the annual grasslands of the Great Central Valley and the low hot valleys of the inner Coast Ranges of California (Burcham 1957). Both are alien species that were introduced in the 19th century. They, along with other annuals of Mediterranean origin, have largely supplanted the perennial grasses of the pristine California prairies and now constitute a major grazing resource. Recent studies have shown that forage production of the annual grasslands is increased markedly by fertilizers containing nitrogen or combinations of nitrogen with sulfur and phosphorus (McKell, Jones, and Perrier 1962, Jones 1963*b,* Walker and Williams 1963). The unfertilized range usually contains *Erodium* species (Geraniaceae) as the major forb component, but the vegetation becomes dominated by grasses, often *Bromus* species, when the major nutrient deficiencies are eliminated.

Martin (1958) reported that *Bromus mollis* is a particularly responsive species to sulfur fertilization when nitrogen is in good supply. Walker and Williams (1963) found that nitrogenous fertilizers increased the growth of *Bromus mollis* and *Erodium botrys* without altering their proportions in the standing crop. When sulfur was applied too, however, dominance shifted to *B. mollis.* Two alternate hypotheses were suggested for the response to sulfur: a higher sulfur requirement for *B. mollis;* or the elimination of all nutrient deficiencies permitted *B. mollis* to overtop and shade the *E. botrys.*

Experiments were conducted to study the mechanisms by which *Bromus* species and other tall grasses dominate annual grassland vegetation when fertilized, while Erodiums dominate under more typical infertile conditions. Specifically, the effect of sulfur fertility on competition for light and nutrients between *Bromus mollis* and *Erodium botrys* was investigated.

MATERIALS AND METHODS

Seeds of *Bromus mollis* L. (soft chess) were collected from a typical annual range site on the San Joaquin Experimental Range, Coarsegold, California. Seeds of *Erodium botrys* (Cav.) Bertol. (broad-leaf filaree) were obtained from ant colonies of the species *Veromesser andrei* Mayr. (black harvester ant) on annual range 10 miles west of Dunnigan, California, in the foothills west of the Sacramento Valley.

Plants were grown in a sandy loam soil of the Hebron series. This soil has a pH of 6.1 and a cation exchange capacity of 10.5 meq/100 g soil. It contains 3.6 ppm LiCl (M/10) extractable sulfate sulfur.[2] Nitrogen was added as NH_4NO_3, phosphorus as KH_2PO_4, and sulfur as K_2SO_4. Equivalent amounts of potassium were applied as KCl to the nil and low rate of sulfur treatments.

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All salts were applied in solution prior to planting. The plants were watered with distilled water.

Experiment 1 was done in a controlled environment cabinet maintained at 21°C during the 10-hr light period and at 10°C during the dark period. Average illumination at the soil surface was 2,300 ft-c, as measured with a Weston illuminometer, Model 756. Light was supplied by fluorescent tubes supplemented with incandescent bulbs. Plants were grown in clay pots 20 cm in diameter and 10 cm deep lined with a polyethylene sleeve. Pots were placed on saucers and free drainage was permitted. Each pot contained 1,700 g Hebron soil mixed with 1,500 g washed river sand. Fertilizer treatments were sulfur at 0, 15, and 50 ppm soil, and nitrogen at 25 and 125 ppm soil, in factorial combinations. Each species was grown in pure stands and also in a 1:1 mixture with each fertilizer treatment, in three replications. Seeds were sown on the soil surface and covered 5 mm deep with washed sand. After emergence, a wire ring, 10.8 cm in diameter, was placed in the center of each pot, delimiting the future harvest area. Stands were thinned to 31 plants/dm² so that all pots contained the same total number of plants. Plants were harvested 30 days after emergence, and dry weights, Kjeldahl nitrogen, total sulfur, and sulfate-sulfur were determined on the plant material.

Experiment 2 was done in the open during April and May 1965, a period of high radiation (mean 606 cal/cm² per day) and moderate temperatures (mean maximum 26°C), except for the 7 days just after emergence (263 cal/cm² per day and 16°C). Containers used were steel cans 10.5 cm in diameter by 35 cm tall lined with a polyethylene sleeve. Free drainage was permitted. Each container was filled with 3,225 g of a Hebron sandy loam soil and fertilized at the rate of 100 ppm nitrogen and 38 ppm phosphorus. There were two levels of sulfur: none added and 30 ppm. In experiment 2a three plants of *Erodium* were grown surrounded by 3, 12, 48, or 192 *Bromus* plants. Experiment 2b consisted of pure cultures of *Erodium* at 3, 12, and 48 plants per pot and pure cultures of *Bromus* at 3, 12, 48, and 192 plants per pot. Plants were protected from birds by cages made from 1-inch poultry net.

Artificial borders were constructed from galvanized window screen covered by black nylon to simulate the effects of border plants in light interception. The borders were raised as the plants grew so that the upper edge of the screen was at the maximum height of the vegetative canopy. The screen alone transmitted 73% of lateral light. The cloth and screen transmitted 3% of lateral light. The height of the borders was adjusted to provide the outermost plants with a light environment similar to that of the central plants.

Just prior to harvesting, light measurements were made in full sunlight above the canopy and at the soil surface of all pots. In addition, in mixtures of species, the amount of light transmitted to the top of the canopy of *Erodium* was measured. All measurements were made between 10 AM and 2 PM, when the incident radiation was roughly perpendicular to the soil surface. For the measurements, an unfiltered selenium cell, 12.5 mm by 22 mm, attached to a Weston microammeter, Model 1951, was used and calibrated with a Weston illumination meter, Model 756.

At harvest the plants were clipped at the soil surface, placed in polyethylene bags, and stored at slightly above 0°C for subsequent laboratory measurements. The leaf area of the *Bromus* above the *Erodium,* the remaining *Bromus* leaf area, and the leaf area of the *Erodium* were determined with an airflow planimeter (Jenkins 1959). Dry weights were determined for shoots of each species at 14, 28, and 42 days after emergence. Shoot tissue was ground and wet-ashed for the determination of total sulfur.

The low planting densities were irrigated whenever the surface soil appeared dry. Stands of high densities were irrigated once or twice daily, depending on the weather, but appreciable drainage was avoided. During the third harvest interval, high-density high-sulfur treatments received Hoagland's solution, minus micronutrients, at alternate irrigations, and low-density treatments received the same solution less frequently in an attempt to prevent any limitation on growth as a result of nutrient shortages.

In both experiments dry weights were determined after samples had been in a forced-draft oven at 65°C for at least 48 hr. Sulfur determinations were made according to the technique of Johnson and Nishita (1952). Since this method estimates sulfate-sulfur, the analyses for this fraction were made on ground plant material. For determinations of total sulfur, the plant material was wet-ashed to oxidize all reduced sulfur to sulfate before analysis.

Relative growth rate was calculated in the usual manner from $(\log_e W_2 - \log_e W_1)/(t_2 - t_1)$, in which W is the shoot dry weight at time t (Williams 1963). The increase in shoot dry weight is regarded as a process of continuous compound interest, with each growth increment being added to the "capital" for further growth, and is expressed as milligrams increased weight per gram total weight per day.

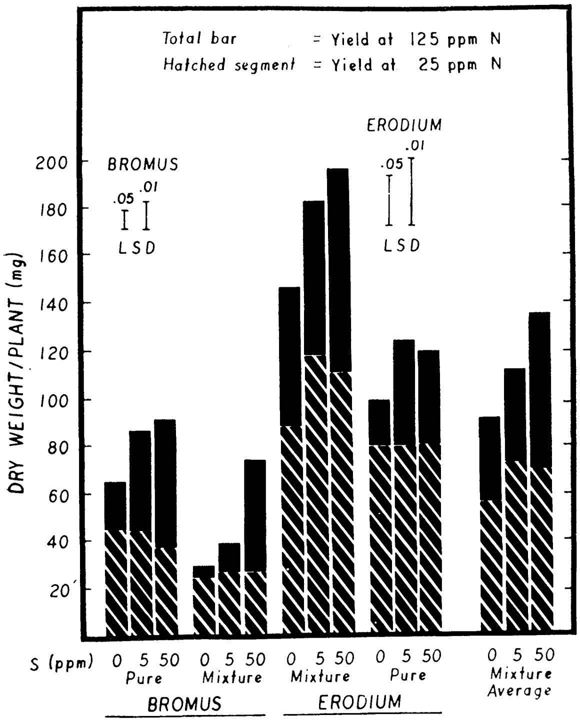

FIG. 1. The effect of sulfur and nitrogen fertilization on *Bromus* and *Erodium* shoot dry weight of individual plants in pure stands and in 1:1 mixtures (experiment 1).

RESULTS

Competition for nutrients in mixtures of equal numbers of Bromus *and* Erodium *(experiment 1)*

Competitive abilities of the species were assessed by comparing growth in mixtures of equal numbers of each species with their growth in pure stands. At the high nitrogen level, maximum dry weight was almost achieved with 5 ppm sulfur (S_5) for both species in pure cultures (Fig. 1). In the mixture, S_5 produced a highly significant increase in *Erodium* yield and a small but significant increase in *Bromus* yield. Sulfur at 50 ppm (S_{50}) resulted in no significant increase in *Erodium* over the S_5 treatment, whereas the yield of *Bromus* in the S_{50} treatment was nearly double that at the S_5 treatment, a difference significant at the .01 probability level.

The interpretation of these growth responses is aided by chemical analysis of plant tissue. Jones (1963*a*) found the critical concentration of sulfate-sulfur for the shoots of these species to be in the range of 200 to 400 ppm dry basis. i.e., growth is a function of sulfate-sulfur concentration at tissue levels less than 200 ppm dry basis, while growth becomes limited by other factors at concentrations above 400 ppm.

TABLE 1. Sulfate-sulfur concentration in shoots of *Bromus* and *Erodium* in pure stands and in 1:1 mixtures (experiment 1)

Nutrient additions		Sulfate-sulfur (ppm)			
		Bromus		*Erodium*	
N(ppm)	S(ppm)	Pure	Mixture	Mixture	Pure
25	0	170	40	100	130
25	5	1,520	1,040	1,120	1,370
25	50	2,000	1,540	1,580	1,860
125	0	40	40	50	50
125	5	320	130	400	380
125	50	1,320	1,400	1,700	1,200

At the high nitrogen level plus S_0 the concentration of sulfate-sulfur in both species was 40–50 ppm both in pure stands and in the mixture, indicating severe sulfur deficiency (Table 1). In the S_5 treatment the *Bromus* component of the mixture, which had a moderate dry weight increase, had a sulfate-sulfur concentration of 130 ppm. The *Erodium* component contained 400 ppm. The S_{50} treatment, which produced a marked increase in *Bromus* dry weight, had a sulfate-sulfur concentration of 1,400 ppm. Figure 1 and Table 1 indicate that, at the high nitrogen level with sulfur in short supply, *Erodium* was able to increase in dry weight at the expense of *Bromus*. With *Bromus*, maximum growth response to sulfur occurred only when sulfur was added in amounts in excess of the requirements of the associated *Erodium*.

At the low nitrogen level there were no significant dry-weight increases in pure stands as a result of additions of sulfur (Fig. 1). In the mixture the addition of 5 ppm sulfur produced an increase of 25% in *Erodium* weight. However, weight of the *Bromus* component of the mixture did not increase. Although it might seem that competition for nitrogen occurred here, this interpretation was not supported by tissue analysis.

The response to nitrogen was strikingly different for the two species grown in mixture (Fig. 1). Increases in *Erodium* yield due to the applied nitrogen did not differ significantly among sulfur levels, and all yields were significantly higher than at low nitrogen. On the other hand, *Bromus* responses to nitrogen increased significantly with increasing sulfur levels. At S_0 the nitrogen response was not significant. Although the response to nitrogen at S_5 was significant at the .05 level, the increase was greatest at the highest sulfur level (S_{50}). This is further evidence that *Erodium* was able to exploit the limited sulfur pool to the detriment of the associated *Bromus*.

Effect of Bromus *population density and sulfur fertility on growth of* Erodium (experiment 2a)

Under natural conditions *Bromus* plants greatly outnumber *Erodium* plants generally (Biswell and Graham 1956, Sumner and Love 1961). In this experiment the effect of density of *Bromus* plants on the growth of associated *Erodium* at high and low sulfur levels was measured with particular attention to the structure of the leaf canopy and competition for light. Ideally, there would have been one *Erodium* plant per pot in order to eliminate *Erodium* intraspecific effects. It was judged, however, that random variation among single *Erodium* plants might have been excessive. Thus, three plants were used as a compromise between minimizing intraspecific competition and minimizing error variation. The densities of 3 *Erodium* and 3, 12, 48, and 192 *Bromus* plants per pot are equivalent to 3.8 *Erodium* and 3.8, 15.5, 62, and 248 *Bromus* plants per dm^2, respectively.

Shoot yields of *Erodium* in mixtures, relative to the control (3 *Erodium,* 0 *Bromus*), were suppressed by increasing population density and duration of growth (Fig. 2). At both sulfur levels, shoot yields of *Erodium* were a function of the number of associated *Bromus* plants. At successive harvest dates, progressively lower densities of *Bromus* suppressed *Erodium* yields relative to the *Erodium* control. The effects of *Bromus* density and duration of growth period were much greater, however, at the high sulfur level than at the low sulfur level. The mixtures with high sulfur tended toward grass dominance, culminated at the highest *Bromus* density by high *Erodium* mortality by 42 days. In contrast to this progressive decline in the *Erodium* component in all mixtures at high sulfur, there was evidence of the establishment of a rather stable *Erodium* content in the low-sulfur mixtures (Table 2).

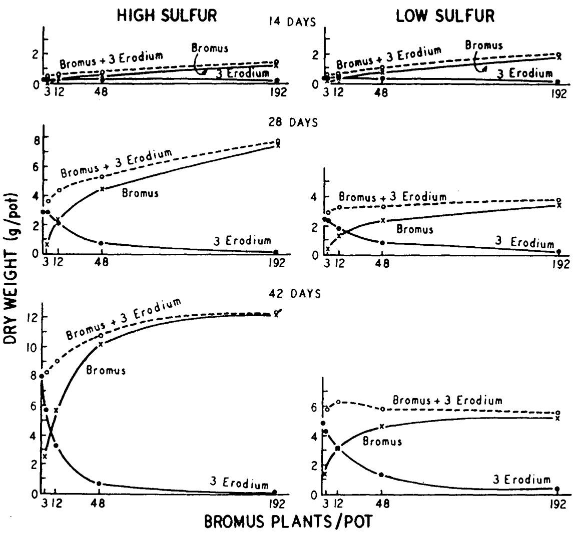

Fig. 2. Effect of number of *Bromus* plants in mixtures with three *Erodium* plants on the shoot dry weight of each species component and their sum at two sulfur levels (experiment 2a).

Table 2. Percentage dry weight of *Erodium* in mixtures of three *Erodium* plus various numbers of *Bromus* plants per pot after 14, 28, and 42 days (experiment 2a)

Number of *Bromus* plants	High sulfur			Low sulfur		
	14 days	28 days	42 days	14 days	28 days	42 days
3	87	82	70	84	84	77
12	53	47	37	53	58	50
48	25	15	6.3	26	29	23
192	4.6	2.5	0.1	7.7	7.2	7.3

Table 3. Total sulfur concentration in shoots of *Erodium* and *Bromus* in pure stands and mixtures (experiment 2)—expressed in percentage

	Plants per pot		High sulfur			Low sulfur		
	Bromus	*Erodium*	14 days	28 days	42 days	14 days	28 days	42 days
Pure *Erodium*	0	3	0.37	0.30	0.26	0.21	0.15	0.07
Erodium in mixture	3	3	.32	.30	.25	.20	.14	.04
	12	3	.36	.33	.34	.20	.12	.07
	48	3	.38	.32	.40	.18	.12	.07
	192	3	.33	.45	.32	.12	.10	.13
Bromus in mixture	3	3	.25	.34	.21	.20	.16	.06
	12	3	.34	.32	.24	.18	.10	.06
	48	3	.29	.32	.26	.28	.11	.07
	192	3	.32	.33	.26	.19	.09	.06
Pure *Bromus*	3	0	.31	.28	.23	.28	.24	.07
	12	0	.27	.33	.21	.30	.10	.07
	48	0	.31	.32	.27	.25	.09	.06
	192	0	.31	.27	.24	.18	.11	.06
				LSD 5% = .05*				

*LSD for the low sulfur mixtures and the three plants per pot pure stands for both species.

At the high sulfur level, the total sulfur concentration in the plants was never less than 0.2% for either species (Table 3), the approximate critical concentration of total sulfur for these species (McCown 1966). Hence, it is very unlikely that growth of *Erodium* was limited by sulfur deficiency. Rather, the taller growing grass assumed a competitive role in controlling *Erodium* growth by shading. With the high sulfur level, *Bromus* developed a substantial leaf canopy above the *Erodium* foliage (Fig. 3). At the higher population densities the leaf-area index values (leaf area, one side only, subtended per unit ground area) of *Bromus* foliage above the *Erodium* foliage were several to many times those for the *Erodium.*

Description of the light environment of *Erodium*

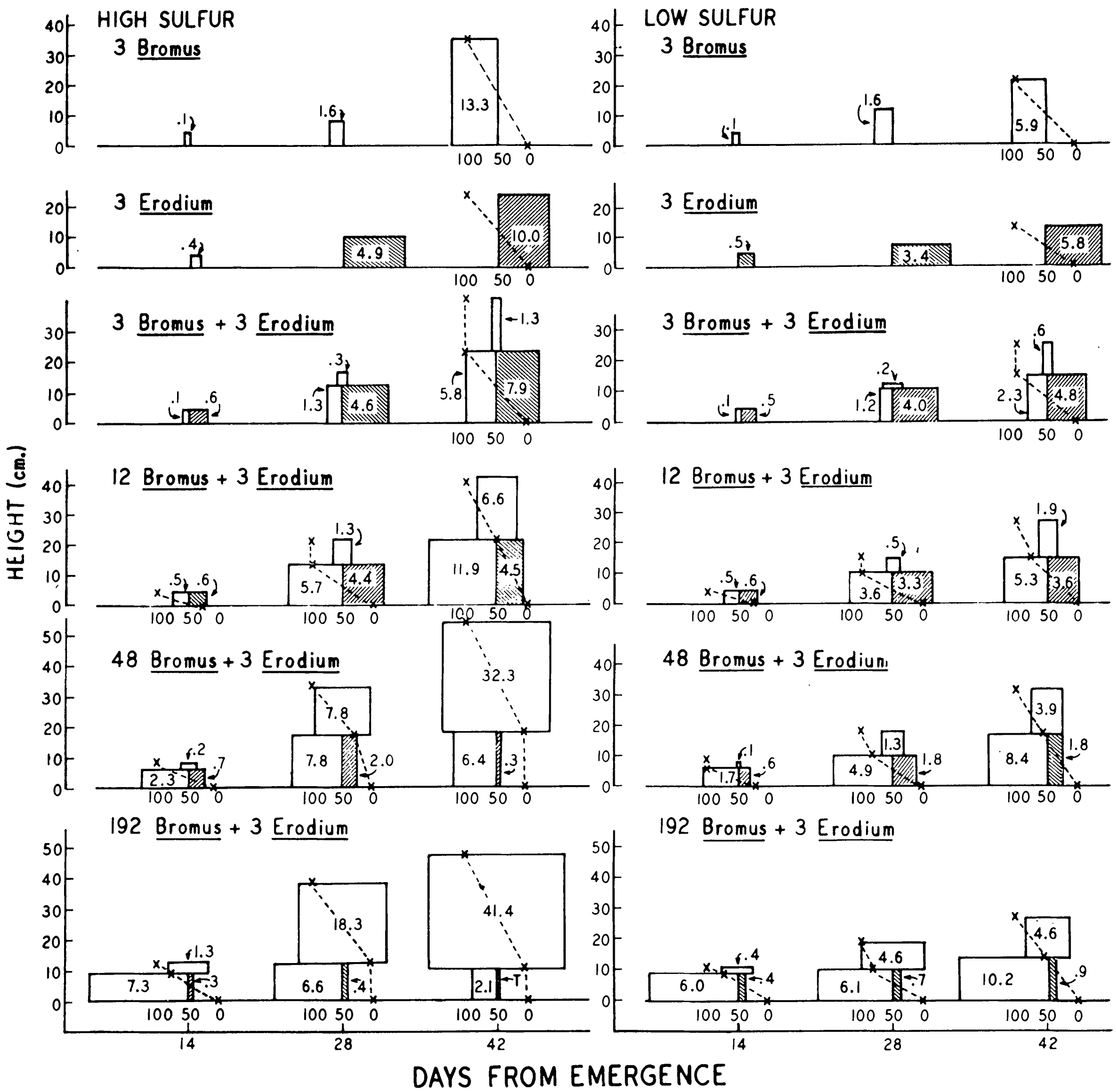

FIG. 3. Foliage canopy structure of pure stands and mixtures of *Bromus* and *Erodium* (hatched). The areas of the rectangles are proportional to the indicated leaf-area index values. In mixtures, *Bromus* leaves were measured in two strata, above and below the average height of the associated *Erodium*. Dotted lines represent illumination as percentage of full daylight (experiment 2).

was difficult because insertion of the photo cell into the canopy of very erect grass laminae produced an opening, resulting in erroneously high readings. Nevertheless, the illumination diagrams in Fig. 3 are useful for qualitative interpretation of the *Erodium* growth responses. The ability of *Bromus* to intercept light and, hence, cast deep shade on the associated *Erodium* is evident. Thus, increases in superior *Bromus* leaf area with increases in *Bromus* density and age appear to account for the corresponding suppression of *Erodium* yields.

At the low sulfur level, sulfur deficiencies were acute in both species in the mixture, but there was no evidence of either species gaining a disproportionate share of available sulfur (Table 3). The degree of shading of the *Erodium* by the associated grass was markedly less at low sulfur than at the high level (Fig. 3). This was reflected in the relative growth rates (Fig. 4). In contrast to the results at high sulfur, relative growth rates of *Erodium* generally exceeded those of *Bromus* at low S during the 14–28-day interval, and were exceeded by *Bromus* by only a moderate degree at low S during the 28–42-day interval.

Yield-density relationships of pure cultures of Bromus *and* Erodium *(experiment 2b)*

Pure culture yield-density relationships were determined as one means of predicting the influ-

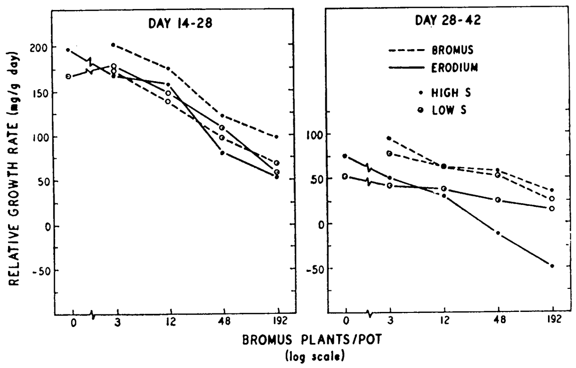

FIG. 4. Relative growth rates of the components of mixtures of three *Erodium* plants + various numbers of *Bromus* plants at two sulfur levels (experiment 2a).

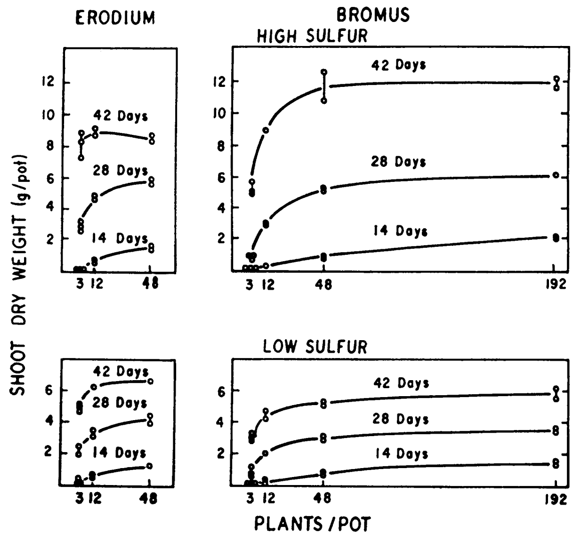

FIG. 5. The relationship of total shoot dry weight to population density in pure stands of *Bromus* and *Erodium* at two sulfur levels (experiment 2b).

ence of density on the competition of species in mixtures. At all harvest dates, *Erodium* was more productive than *Bromus* at the lower densities (Fig. 5). At low sulfur, *Erodium* was more productive than *Bromus* at all comparable densities, and moreover, 48 *Erodium* plants were more productive than 192 *Bormus* plants at the later harvest dates. At high sulfur, however, *Bromus* yield exceeded maximum *Erodium* yield by 33%.

This marked difference in production under light-limiting conditions appears to be related to differences in relations between leaf-canopy structure and light interception. The average extinction coefficients were 0.4 for *Bromus* and 0.9 for *Erodium*. These values were calculated from light-interception data and the amount of leaf area penetrated (Fig. 3) using the Bougeur-Lambert function:

$$I = I_0 e^{-kL}$$

where I and I_0 refer to the illumination beneath and above the foliage, k is the extinction coefficient, and L is the leaf area index (Loomis, Williams, and Duncan 1967). The lower extinction coefficient for *Bromus* is a consequence of its upright habit of leaf display and is associated with more uniform vertical distribution of light in the foliage and improved efficiency of light utilization in dense foliage. The optimum leaf area index (producing the maximum growth rate) was between 20 and 25 for *Bromus*, and between 5 and 10 for *Erodium*. Hence, under light-limiting conditions, *Bromus* was more productive than *Erodium*, because of an upright leaf arrangement that allowed deeper penetration of light into the leaf canopy, allowing a much higher leaf-area index and greater net photosynthesis.

DISCUSSION

Competition between Bromus mollis *and* Erodium botrys

In the present study, when dry weight yields produced by *Erodium* and *Bromus* in mixtures were compared with the production by equivalent numbers of plants in pure stands, *Erodium* was always favored and *Bromus* was depressed at least slightly by the mixture (Fig. 1). Such comparisons between mixtures and pure stands cannot be made directly in the case of the addition mixtures of experiment 2a. Even so, "actual yields" in mixtures can be compared with "expected yields" in pure stands of comparable density by interpolation from pure stand yield-density curves (Fig. 6) according to the method suggested by Black (1960). Actual yields exceeded expected yields for *Erodium*, while the opposite was true for *Bromus* (Table 4).

In 75% of the studies that Donald (1963) reviewed concerning associated growth of species in pairs, the production per plant of one of the species was increased and that of the other decreased relative to plants in pure stands of equal density. In his words, "One of the species is the aggressor, able to exploit more than its 'share' of the factors of the environment, while the other is suppressed because it is able to secure only a lesser part of the light, water, or nutrients." On the basis of the above comparisons we might state that *Erodium* was the "aggressor" and that the growth of *Bromus* was lessened by its association with *Erodium*. This tentative conclusion, in view of the demonstrated superiority of *Bromus* in competing for light in mixtures, raises the question of whether comparison of performance in mixtures with that in pure cultures is an appro-

TABLE 4. Comparisons of shoot dry weight of *Bromus* and *Erodium* components of mixtures (actual) with estimated yield[a] of an equivalent number of plants per pot in pure stands (expected) in experiment 2

Plants per pot	High sulfur			Low sulfur		
	Expected[a] (g/pot)	Actual (g/pot)	Diff. (%)	Expected[a] (g/pot)	Actual (g/pot)	Diff. (%)
3 *Bromus*...........	3.45	2.52	−27	1.86	1.26	−32
3 *Erodium*..........	4.20	5.83	+39	2.85	4.23	+48
12 *Bromus*..........	7.20	5.76	−20	3.72	3.12	−16
3 *Erodium*..........	1.74	3.24	+86	.42	3.06	+143
48 *Bromus*..........	11.00	10.00	− 9	4.80	4.66	− 3
3 *Erodium*..........	.51	.69	+35	.39	1.35	+246

[a]Interpolated by means of plant weight: density curves in Fig. 6.

priate measure of the interspecific competitive relationships in this case where *Bromus* and *Erodium* differ markedly in their responses to crowding in pure cultures.

Figure 7 shows the relationships between the logarithm of the weight of individual plants and the logarithm of population density in the mixtures. The slope of the log/log regression is proportional to the intensity of competition (Harper 1961). Although *Erodium* plants were always larger than *Bromus* plants at the low sulfur level, the slopes of their log weight-log density curves were similar over the range of population densities studied. This indicates that increase in *Bromus* density resulted in increases in competition which had the same relative effect on both species. However, at high sulfur, increasing the number of

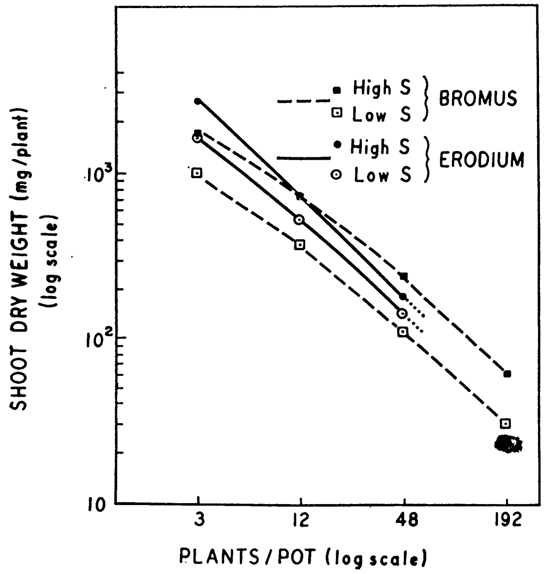

FIG. 6. The effect of sulfur level on shoot dry weight per plant at several population densities in pure stands of *Bromus* and *Erodium* 42 days after emergence (experiment 2b).

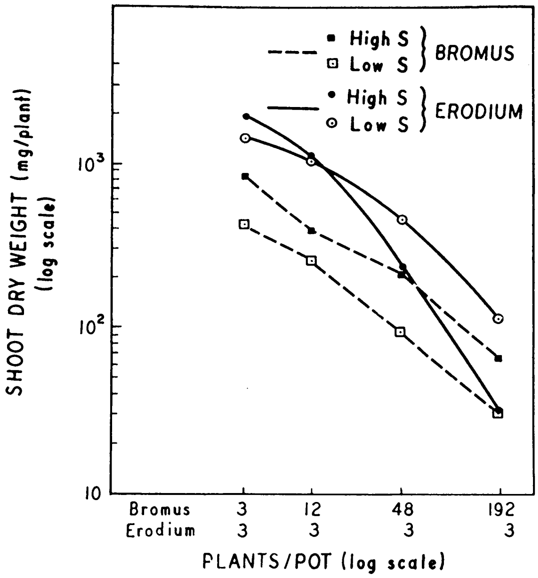

FIG. 7. The effect of sulfur level on the shoot dry weight per plant in *Bromus* and *Erodium* mixtures 42 days after emergence (experiment 2a).

Bromus plants in the mixture reduced weight per plant of *Erodium* more than increasing the number of *Eroduim* plants (from comparison of Fig. 6 and 7). Evidently, *Bromus* was able to exploit the light environment in pure stands much more successfully than could *Erodium*. Hence, the relative advantage to *Erodium* in the mixture was due not to any "aggressive" characteristics but rather to the fact that *Erodium* was merely a poorer competitor in pure culture than in equivalent population densities in mixtures.

Another fruitful approach to the competitive relationships of mixtures of *Bromus* and *Erodium* can be made through use of the growth rates of each species component in relation to various environmental factors. In experiment 2a, although there were three *Erodium* plants, the effects of competition among *Erodium* plants in most instances was small in relation to competition with the associated *Bromus*. When competition was for light only (with high sulfur), relative growth rates for *Bromus* exceeded those for *Erodium* at all densities during both harvest intervals, with the difference increasing with increases in *Bromus* density and age (Fig. 4). When sulfur supply was limiting to growth, relative growth rates for *Erodium* exceeded those for *Bromus* at low densities during the first harvest interval. With increased *Bromus* density, age, or both, relative growth rates for *Bromus* exceeded those for *Erodium*. Although *Erodium* was the aggressor when competition for light was minimal, presumably because of its initially greater leaf area (McCown

1966), *Bromus* always became the aggressor when competition for light became appreciable.

A major purpose of these studies was to determine whether *Erodium* is a more successful competitor for sulfur than *Bromus*. In experiment 1 *Erodium* was depriving *Bromus* of sulfur when the supply was limited (Fig. 1). In an ancillary experiment, rates of root elongation of isolated plants were measured in sand-filled glass tubes inclined at 60° from horizontal. One week from the onset of germination *Erodium* had penetrated 18 cm, while *Bromus* had reached a depth of only 6 cm (Fig. 8). It is reasonable to conclude that *Erodium* exploited limited sulfur supplies to the detriment of *Bromus* simply because *Erodium* roots "got there first."

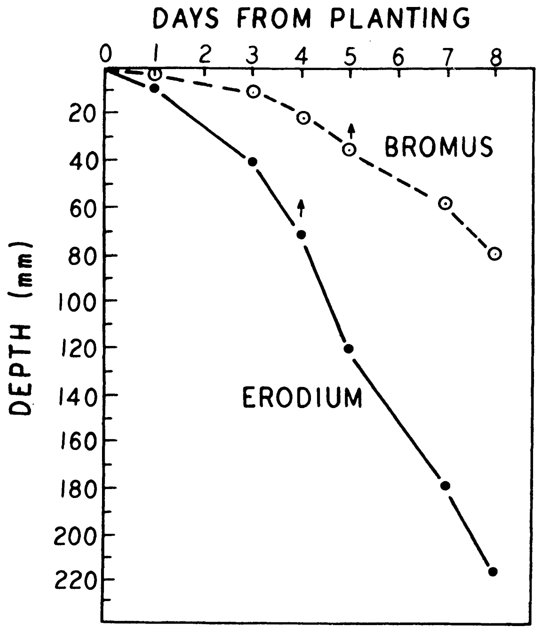

FIG. 8. Penetration of roots of *Bromus* and *Erodium* into moist sand. Arrows indicate seedling emergence.

When the soil supply of one or more nutrients is inadequate, leaf canopy above the *Erodium* is restricted. Under such conditions the handicap of *Erodium*'s low stature is minimized. On the other hand, an early rapid growth rate and a deep rooting habit provide *Erodium* an advantage when nutrients are scarce. It has been shown in lysimeter studies that sulfate is leached readily from coarse-textured soils (McKell and Williams 1960). Annual plants with shallow rooting habits may experience sulfur deficiency early in the season, but recover later as sulfate is released by the decay of organic matter. Deep-rooted perennial plants on the same soils may never experience any deficiency, having access to sulfate accumulated in the clay subsoil (Jordan and Bardsley 1958). In the present studies, the pots provided an environment in which the normally deeper rooted *Erodium* had access only to the same sulfur reservoir as did the *Bromus*, and *Erodium* excelled in competing for sulfur because of its more rapid early growth. This same situation presumably occurs in many areas of annual vegetation where only a few inches of soil overlie bedrock (Storie 1951), or in early season when rainfall may have wetted only a shallow portion of the profile.

Comparisons of benefits of mixtures and pure stands

Unlike sown crops, *Bromus mollis* and *Erodium botrys* rarely exist in pure stands except on relatively small areas (as part of the mosaic pattern of the vegetation). However, the relative proportions of grass and *Erodium* in a sward may vary tremendously.

Any association of species that results in greater utilization of the environmental resources, and consequently in greater yield than a pure stand of any component, is a beneficial mixture. However, such mixtures occur only infrequently (Donald 1963). In the studies reported here there was no instance in which a mixture produced significantly more dry matter than a pure culture at the same density.

The total density of the mixtures and of each pure stand must be equal in order to make comparisons as above. In experiment 2b, yields of pure stands of densities equal to the mixtures can be extrapolated from the yield:density curves (Fig. 6). Comparisons of yields of pure stands and mixtures (Table 5) revealed that although the production by the mixture occasionally equaled that of the better pure stand, it never exceeded it appreciably. These results indicate that maximum production under optimum nutrient (and moisture) conditions is achieved with pure stands of *Bromus*. Mixtures of *Bromus* and *Erodium* under such conditions tended to become pure stands of *Bromus* (Table 2). At low sulfur, the maximum aboveground yield of *Erodium* was higher than that of *Bromus* in pure stands and, in general, slightly higher than in the mixtures (Table 5). Thus, from the standpoint of dry matter production under adverse fertility conditions, a large *Erodium* component would seem to be beneficial.

Even when a mixture is not beneficial in terms of total dry matter yield, it may be beneficial in other ways. If the average mutual depression of species in mixtures is less than in pure stands, the mixture might be considered beneficial. A means of assessing this was proposed by G. A. McIntyre and discussed by Donald (1963). This

TABLE 5. Shoot dry weight (grams/pot) of pure stands and of mixtures of *Bromus and Erodium* (experiment 2)

Plants/pot	High sulfur			Low sulfur		
	Pure *Bromus*[a]	Mixture[b]	Pure *Erodium*[a]	Pure *Bromus*[a]	*Mixture*[b]	Pure *Erodium*[a]
6	6.9	8.4	8.3	3.7	5.5	5.7
15	9.0	9.0	8.6	4.7	6.3	6.3
51	11.5	10.8	8.7	5.4	6.0	6.7
195	12.2	12.3	—	5.9	5.5	—

[a]Yields in pure stands were obtained by interpolation from yield: density curves in Fig. 6.
[b]Actual yields of mixtures of three *Erodium* plants with 3, 12, 48, and 192 *Bromus* plants.

technique can be illustrated using the data from the "3 *Bromus* + 3 *Erodium*" mixture at low sulfur in experiment 2b. The dry weight of a single *Erodium* plant was 1.41 g (Fig. 7). It can be interpolated from Fig. 6 that a plant this size would have developed in a pure stand of 3.7 plants per pot. Considering that there were three *Erodium* plants in the mixture, the three *Bromus* plants in the mixture had an effect equivalent to 0.70 *Erodium* plants. Similarly, the mean yield of *Bromus* plants in the mixture was 0.42 g, a weight which would have been obtained in a pure stand of 10 plants per pot. Thus, three *Erodium* plants had an effect equivalent to seven *Bromus* plants. In symbolic terms:

Competitive effect on 3 E plants: $3B = 0.70E$; $(E/B)_1 = 4.3$

Competitive effect on 3 B plants: $3E = 7.0B$; $(E/B)_2 = 2.3$

The ratio E/B expresses the competitive effect of one plant of *Erodium* in terms of *Bromus* equivalents. The $(E/B)_1$ indicates that 4.3 *Bromus* plants had an effect on an *Erodium* plant equivalant to that of another *Erodium* plant. The $(E/B)_2$ indicates that one *Erodium* plant had an effect on a *Bromus* plant equivalent to that of 2.3 *Bromus* plants. In other words, in this mixture *Bromus* had a small effect on *Erodium*, and *Erodium* had a large effect on *Bromus*, as demonstrated by the difference between the equivalence factors (E/B). An index of the overall benefit of the mixture can be calculated as the ratio of the equivalence factors 1 and 2. Thus the "competition index" $[(E/B)_2/(E/B)_1]$ in this case is 0.54. The competition index can be calculated independent of the equivalence factors as

$$\frac{\text{Pure culture equivalents}}{\text{Actual number of plants}} = \frac{7.0 \times 0.70}{3 \times 3} = \frac{4.9}{9} = 0.54$$

The equivalence factors and competition indices of the mixtures of experiment 2a are presented in Table 6. A competition index of less than 1.0 indicates that the interplant competition is less than would be predicted by the yields in pure stands when comparisons are made on the basis of the products of the numbers. A value of 1.0 or larger indicates a mixture of no benefit or one of detrimental effect. Hence, mixtures of *Bromus* and *Erodium* at a high sulfur level were not beneficial, but at low sulfur were beneficial.

TABLE 6. The equivalence factors (E/B) and competition indices (CI) for mixtures of *Bromus* (B) and *Erodium* (E) (experiment 2)

Mixture	High sulfur		Low sulfur	
	E/B	CI	E/B	CI
3 *Bromus* 3 *Erodium*	1) 2.3 2) 2.3	1.0	1) 4.3 2) 2.3	0.54
12 *Bromus* 3 *Erodium*	1) 2.5 2) 2.8	1.1	1) 4.6 2) 2.2	.48
48 *Bromus* 3 *Erodium*	1) 1.4 2) 2.7	1.9	1) 4.4 2) 2.0	.45

The method devised by Black (1960) for assessing the effects of interspecific competition in a mixture by comparison with pure-stand yields is useful in understanding the meaning of McIntyre's competition index (Table 4). In general, *Erodium* was favored by being in a mixture (positive differences), while *Bromus* was depressed (negative differences). The effect of *Erodium* on *Bromus* was about the same at high as at low sulfur. However, the enhancement of *Erodium* growth in the mixture was markedly greater at low sulfur than at high sulfur. At low sulfur the increase in *Erodium* was much greater than the decrease in the grass. This net favorable interaction is reflected in competition index values of less than 1.0. Since no direct correspondence is apparent between the schemes of Black and McIntyre, it is not surprising that, although the effects of competition were qualitatively similar, the ratio of *Erodium* increase to *Bromus* decrease at high sulfur was so much less than at low sulfur that the competition indices exceeded 1.0.

An inference of practical import can be drawn from these results. The maintenance of *Erodium* as a component of annual grassland vegetation is desirable particularly on soils where fertilization to enhance grass production is uneconomical. Moreover, a large part of the grazeable forage is contributed by *Erodium* in years when the growth of grasses is curtailed by drought (Heady 1961). Thus, a mixture of these species is beneficial in that it provides a buffering effect against moisture or nutritional inadequacies of the environment.

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