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COMPETITION FOR SULFUR BY THREE ANNUAL-RANGE SPECIES IN RELATION TO TEMPERATURE[1]

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Abstract. Competition for sulfur among *Trifolium hirtum, Bromus mollis,* and *Erodium botrys* was studied under adequate (20 lb./acre) and inadequate (5 lb./acre) levels of sulfur and three temperatures (10°, 15.5°, and 21.1°C) under controlled environment conditions. At low levels of sulfur there was little difference in yield or sulfur uptake among the three species with regard to temperature when grown in mono-, di-, or trispecific combinations. In general, both sulfur uptake and yield increased slightly with increasing temperature. At the adequate sulfur level there was a large increase in yield and sulfur uptake of *T. hirtum* both when grown alone and in combination with other species. This increase was most marked at higher temperatures; it was reduced by the presence of *B. mollis,* but was unaffected by the presence of *E. botrys*. The growth and sulfur uptake of *B. mollis* was increased somewhat by the presence of *T. hirtum,* but was unaffected by the presence of *E. botrys*.

INTRODUCTION

Growth of annual species in the annual rangelands of California takes place in an environment of intense competition. Conditions of soil moisture, temperature, and availability of nutrients are not always favorable for seed germination and the survival of adequate numbers of desirable forage seedlings. Differential germination and survival of groups of annual plants have been recognized in common parlance by referring to certain years as "clover years," "filaree years," or "grass years." Such rapid changes at the beginning of each growing season indicate the dynamic nature of the annual range and also point to the need for better information concerning the factors that control changes in species composition.

In the field all possible combinations of species may be growing together, and the type and degree of competition for various nutrients could well be influenced by physical factors of the environment. To understand better the response pattern of three annual forage species (*Trifolium hirtum* All. (rose clover), *Erodium botrys* (Cav.) Bertol. (filaree), and *Bromus mollis* L. (soft chess)), competition experiments were conducted in controlled environment chambers with and without adequate levels of sulfur. With better understanding should come a knowledge of opportunities for some control of composition through such practices as fertilization, chemical application, and grazing management.

LITERATURE REVIEW

The response of individual plants to the environment and to competition from other individuals of the same and different species is a complicated process. In annual rangelands such competition is particularly intense during the early part of the growing season. Environmental stress during this period often causes reduced growth rates, and such stress may differentially affect various species. For instance, McKell, Wilson, and Williams (1962) showed that annual forage legumes introduced to California produced higher yields than native forage legumes over a range of temperatures. At a low temperature the addition of phosphorus fertilizer enhanced the growth of some native legumes to a greater extent than some introduced legumes; at a higher temperature the reverse effect occurred.

Annual range soils in California are often deficient in sulfur. The application of sulfur fertilizers not only increases the total forage production, but also produces changes in species composition (Bentley and Green 1954, Walker 1955). Such changes are of particular interest in annual pastures because a new stand of plants must start each year.

In general, legumes have a higher requirement for sulfur than many grasses and forbs (Jones 1964, Sprague 1964). The different requirements for sulfur among annual pasture species and the yield responses are often spectacular. Jones (1963) compared the response of five species to sulfur during the spring growing season and found yield differences as great as 600% during active growth. Subterranean clover (*Trifolium subterraneum*) was shown to be a poor competitor for sulfur when sulfur fertility levels were low. In a growth chamber study with S^{35} McKell and Wilson (1963) found a difference in sulfur uptake between *Trifolium hirtum* and *T. subterraneum* at 10° and 15.5°C, indicating that *T. subterraneum* functions better in obtaining sulfur at low temperatures than does *T. hirtum.*

In many years the availability of sulfate sulfur in the soil may not coincide with the most favorable

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temperatures for growth. McKell and Williams (1960) found that in a year of above-average rainfall over 80% of the leachable sulfate had been lost from the soil in lysimeters before active clover growth was initiated in the spring. In a subsequent study Williams, McKell, and Reppert (1964) found that in years of below-normal rainfall gypsum-fertilized clover plants accumulated significantly higher amounts of sulfur, but because of limited rainfall forage yields were no greater than from unfertilized plants.

Very often the principal factors controlling the composition of species in an annual range or pasture operate early in the period of plant growth. At this time, depending on the earliness or lateness of autumn rains, temperatures may be low and the amount of sulfur may also be low because of the low level of biological activity that makes sulfate sulfur available.

Methods

Two separate experiments were conducted, the first with no sulfur applied to the soil and the second with an adequate level of sulfur supplied.

Four-inch clay pots were filled with 550 g of screened Vista sandy loam. This sulfur-deficient soil was obtained from an undisturbed site at the San Joaquin Experimental Range in Madera County, California. Characteristics and chemical analysis of this soil were reported by McKell and Williams (1960). Germinated seeds of *Trifolium hirtum, Erodium botrys*, and *Bromus mollis* were space-planted in the pots according to the following plan: monospecific competition, six plants per pot; bispecific competition, three plants of each species per pot; trispecific competition, two plants of each species per pot. Two additional pots of the trispecific combination were planted to provide extra material for chemical analysis. Three replications each of the above eight planting combinations were grown in each of three controlled environment chambers.

Seedlings were allowed to grow under normal greenhouse temperatures for 2 weeks and were then fertilized with a small amount of nitrogen (20 lb./acre NH_4NO_3) because of the very low nitrogen status of the soil. One week later the plants were transferred to growth chambers maintained at 10°, 15.5°, and 21.1°C with an 8-hr daylength. Plants were harvested after 45 days, ovendried, weighed, and prepared for sulfur analysis. The sulfur analysis[5] followed procedures outlined by Johnson and Nishita (1952).

The experiment was repeated with the same species combinations, blanket nitrogen application, and the same temperatures, but the soil in each pot was fertilized at a rate of 20 lb. of sulfur per acre. This amount has been reported previously as adequate for Vista sandy loam (Bentley and Green 1954). Calcium sulfate was used as the sulfur source. Pots were kept in the greenhouse for 5 weeks before distribution to the growth chambers in order to obtain larger plants than in the first experiment. The plants were kept in the growth chambers for 42 days. In the first experiment the three replications had to be bulked to obtain sufficient material for the sulfur analysis.

Results

Total yield did not differ among any of the combinations of species when they were grown on sulfur-deficient soil (Table 1). With an adequate level of sulfur there were large differences among the various species combinations. Least productive was grass alone. Intermediate in yield were grass-filaree, filaree alone, the combination of all three species, and clover-grass. The highest yields were obtained from clover-filaree and clover alone.

Yield increases in general were obtained with temperature increases. Such increases were of the order of one-third for each 5-degree rise in temperature. However, inadequate sulfur appeared to restrict any further yield increases between 15.5° and 21.1°C in the low-sulfur experiment.

In the low-sulfur experiment the interaction between species combinations and temperature was not significant at the 5% level (Table 1). However, in the high-sulfur experiment this interaction was significant, indicating that the different species combinations responded differently to the different temperatures. At 10°C differences in the yield per pot among the different species combinations were not significant, but at 21.1°C the differences were large. The increases in yield of grass and filaree alone were not significant at the 5% level.

Even though statistical comparisons cannot be made between plant yields from the first and second experiments, production of clover and filaree was generally increased about one-third when sulfur was supplied at the adequate level. The addition of sulfur in the second experiment appeared to have the greatest effect on the species combinations that included clover. For example, the average yield per pot for *T. hirtum* in the low-sulfur experiment was 0.38 g, and in the adequate-sulfur experiment the average yield was 0.81 g, whereas the yields for *B. mollis* were 0.35 g and 0.37 g, respectively.

The actual uptake of sulfur into the plant tops was obtained by multiplying the concentration of sulfur by the weight per pot (Table 2) or per plant (Fig. 1). Because the replications were bulked for sulfur analysis in the experiment with inadequate sulfur, statistical analysis of the results was not possible.

[5] Grateful acknowledgment is expressed to Mr. Joseph Ruckman, Associate Specialist, Agronomy Department, University of California, Davis, for his assistance in supervising the chemical analysis.

TABLE 1. Yield per pot (g) of annual species in mono-, di-, and trispecific combinations grown at two levels of fertility and three temperatures[a]

Temperature (°C)	Grass	Clover	Filaree	Clover-grass	Clover-filaree	Grass-filaree	Clover-filaree-grass	Mean
				Inadequate sulfur (5 lb./acre)				
10	0.27	0.28	0.30	0.22	0.36	0.18	0.23	0.26x
15.5	0.34	0.50	0.45	0.41	0.41	0.46	0.54	0.44y
21.1	0.44	0.36	0.35	0.37	0.54	0.48	0.39	0.42y
Mean	0.35	0.38	0.37	0.33	0.44	0.38	0.38	
				Adequate sulfur (20 lb./acre)				
10	0.28h	0.43efgh	0.44efgh	0.43efgh	0.44efgh	0.34gh	0.39fgh	0.39r
15.5	0.35gh	0.86b	0.56ef	0.57def	0.80bc	0.51efg	0.62cde	0.61s
21.1	0.47efgh	1.13a	0.62cde	0.82b	0.91b	0.59def	0.76bcd	0.76t
Mean	0.37p	0.81m	0.54no	0.61n	0.72m	0.48o	0.59n	

[a]Values followed by the same letter (s) are not significantly different from each other (5% level). There is no statistical comparison between values in the two experiments. Where no letters are shown, the differences are not significant at the 5% level.

TABLE 2. Sulfur uptake (mg per pot) by annual forage species in mono-, di-, and trispecific combinations grown at two levels of fertility and three temperatures[a]

Temperature (°C)	Grass	Clover	Filaree	Clover-grass	Clover-filaree	Grass-filaree	Clover-filaree-grass	Mean
				Inadequate sulfur (5 lb./acre)				
10	0.79	0.51	0.50	0.71	0.60	0.28	0.14	0.50
15.5	0.55	0.84	0.36	0.75	0.59	0.17	0.28	0.63
21.1	0.95	1.32	0.36	0.77	1.41	1.26	1.14	1.03
Mean	0.76	0.89	0.41	0.74	0.87	0.87	0.51	
				Adequate sulfur (20 lb./acre)				
10	0.63k	1.29jk	1.02jk	1.24jk	1.13jk	0.64k	1.11jk	1.01a
15.5	0.78k	3.00fg	1.16jk	1.28jk	2.06hi	0.64k	1.65ij	1.51b
21.1	1.32jk	4.691	1.64ij	2.62gh	3.44f	1.06jk	2.54gh	2.47c
Mean	0.91q	2.99m	1.27p	1.71o	2.21n	0.78q	1.77o	

[a]Values followed by the same letter (s) are not significantly different from each other (5% level). Statistics are not available for the inadequate sulfur experiment (see text).

Nevertheless, in most cases uptake of sulfur generally increased with increasing temperature (Table 2, Fig. 1). When the three species were grown together at the lower temperatures, the total uptake per pot (plant tops only) was very low (Table 2), and the uptake per clover plant was particularly low (Fig. 1). The marked increase in sulfur uptake per pot at 21.1°C was largely accounted for by the increase in uptake per clover plant.

With adequate sulfur levels, sulfur uptake per pot increased significantly with increasing temperature, and total uptake per pot differed greatly with different species combinations (Table 2). Clover alone gave the highest uptake, followed by the clover-filaree species combination. The uptake of the clover-grass and the trispecific combination was next, followed by filaree alone. The lowest uptake per pot occurred with the grass alone and the grass-filaree combination.

The species-by-temperature interaction was significant at the 5% level, indicating a differential response of the species combinations to the increase in temperature. The only combinations that gave a significant increase in sulfur uptake per pot were those containing clover. Most of this increase was the result of the almost linear increase in uptake by clover with increasing temperature (Fig. 1). This temperature-induced increase in uptake is little affected by the presence of filaree, but appears to be suppressed by the presence of grass—only slightly in the trispecific combination, but to a greater extent in the clover-grass mixture. The uptake by the grass, on the other hand, appears to be enhanced by the presence

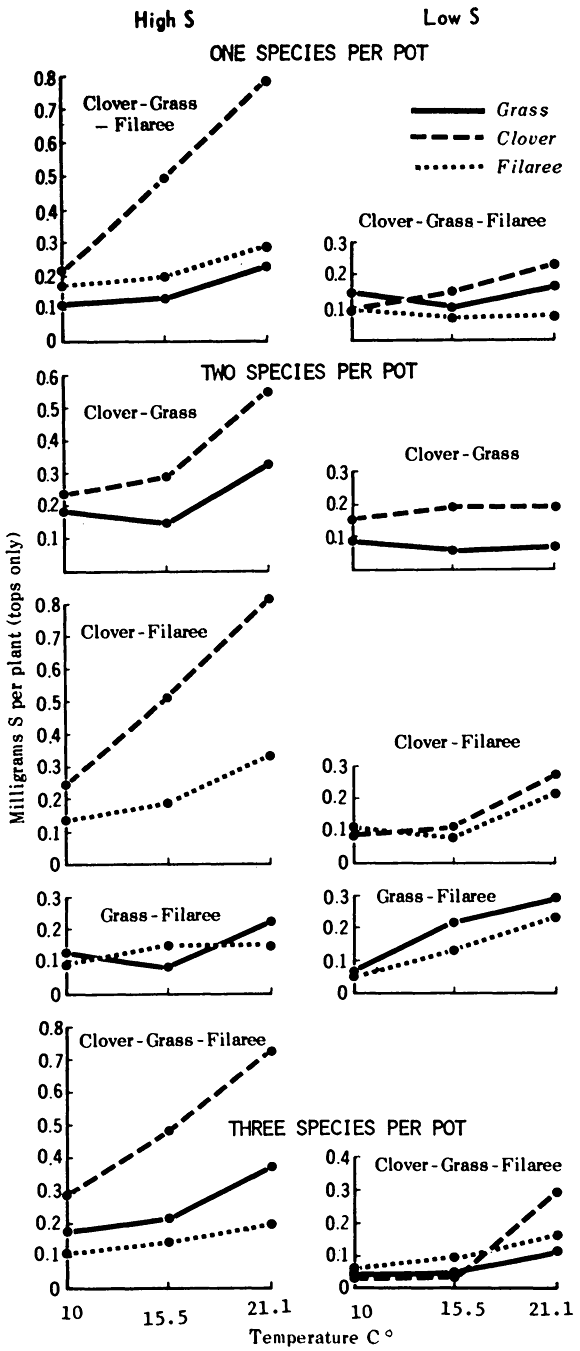

FIG. 1. Mono-, bi-, and trispecific competition for sulfur by *Trifolium hirtum, Erodium botrys,* and *Bromus mollis* at 10°, 15.5°, and 21.1°C.

of the clover but not by the presence of the filaree.

Although no statistical comparison can be made between sulfur uptake in the two experiments, it is profitable to compare the two sets of results. Although the addition of sulfur caused a marked increase in the uptake of sulfur by the clover alone and the filaree alone (Table 2), there was little if any increase in uptake by the grass alone or the grass-filaree combination. When comparing the uptake per plant (Fig. 1), the presence of clover or clover and filaree appears to increase the uptake of sulfur by the grass when extra sulfur is supplied. With the grass-filaree combination, the provision of extra sulfur appears to have little effect on the uptake per plant.

DISCUSSION

When grown in controlled conditions with inadequate sulfur, *T. hirtum* appears to be an average competitor in growth and sulfur uptake when compared with *B. mollis* and *E. botrys.* All three species respond to increases in temperature, but the increased temperature does not markedly increase the growth or sulfur uptake of any one species in competition with any other. In the field, where the seed population in the soil of established species may be very high, one would expect difficulty in the successful introduction of a species such as *T. hirtum* when sulfur is inadequate. Walker and Williams (1963) found that *T. hirtum* grown in sulfur-deficient areas of the Sierra Nevada foothills of California failed to become an important forage species unless the deficiency of sulfur was corrected with at least 100 lb./acre application of gypsum ($CaSO_4 = 20\%$ S).

With the provision of adequate sulfur, the position is quite different. A competitive advantage, both in terms of growth and sulfur uptake, is immediately conferred on *T. hirtum,* and this advantage is enhanced by increasing temperature. Thus, with an early autumn seasonal break and adequate sulfur, a clover-dominant pasture would be expected, but with a later break, when temperatures are lower, less clover and more grass or filaree would be expected as they have a less steep temperature response. Adequate availability of sulfur in the spring is therefore of considerable importance for a high level of annual clover productivity.

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