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GERMINATION AND GROWTH OF SOME SEMIDESERT GRASSLAND SPECIES TREATED WITH AQUEOUS EXTRACT FROM CREOSOTEBUSH[1]

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Abstract. The effects of aqueous extracts from creosotebush (*Larrea tridentata*) material on germination and initial growth of black grama (*Bouteloua eriopoda*), bush muhly (*Muhlenbergia porteri*), and creosotebush were studied. There was no apparent difference among extracts obtained from the various creosotebush plant parts. An aqueous extract from leaves and twigs significantly reduced germination of black grama caryopses, but the germination of bush muhly caryopses and of creosotebush seeds (removed from the carpels) was not affected. Less concentrated extracts did not significantly reduce germination of the test species. However, radicle and plumule growth of black grama and bush muhly were significantly reduced by all extracts. Apparently the relatively low osmotic concentrations or the moderate pH's were not responsible for these reductions in growth.

Comparisons among creosotebush seeds (removed from the carpel) watered with a carpel extract and a water-mannitol solution of the same osmotic concentration, and carpels treated with water indicated that there is a structural characteristic or a non-water-soluble chemical compound in the carpel which inhibits germination of creosotebush. Germination of creosotebush seeds treated with water-mannitol solutions of 1.50, 3.50, 5.00, and 7.00 atm osmotic concentration was significantly reduced as compared to those treated with low concentrations simulating field capacity.

Nutrient solution recycled for 37 days around the roots of creosotebush plants growing in a gravel-sand substratum was not inhibitory to germination or initial growth. In a pot test, creosotebush extracts created a crust on the soil surface which reduced the infiltration rate of water.

Some of the preceding factors may possibly contribute to the degeneration of grassland areas where creosotebush is present.

INTRODUCTION

Creosotebush (*Larrea tridentata* (DC.) Coville) dominates (often in almost pure stands) an estimated 46.5 million acres of sparsely vegetated arid lands from West Texas to California (Platt 1959). Part of the region is semidesert grassland dominated by short grasses of the genera *Bouteloua, Aristida,* and *Hilaria,* and the mid-grass *Muhlenbergia porteri* (Weaver and Clements 1938).

The journals of early explorers, Gregg (1845), Wislizenus (1848), and others, make little or no mention of creosotebush in the semidesert grassland, and in describing the area they make use of such phrases as "a sea of grass," "abundant," and

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"luxuriant" grama grass. Fountain (1885), promoting the settlement of Mesilla Valley in the late 1800's, wrote that thousands of tons of grama hay could be cut along the railroad near Las Cruces. He maintained that a man could purchase a farm in the valley and pay for it with proceeds of hay crops that could be cut and baled on the farm and shipped elsewhere via the railroad. The areas described by the early explorers and by Fountain are now dominated by creosotebush (Fig. 1).

We thought it possible that creosotebush might contain a germination or growth inhibitor which may contribute to the invasion and dominance of creosotebush on grassland. The presence of germination or growth-inhibiting substances in plants is not uncommon. They occur in all parts of

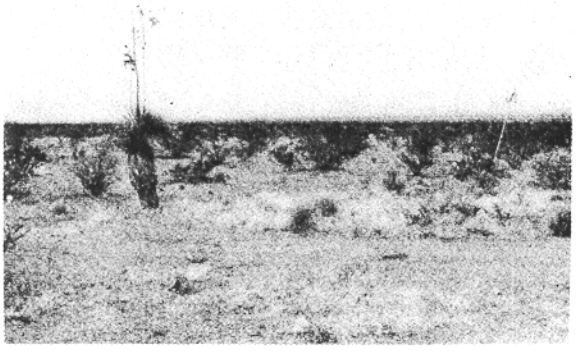

FIG. 1. Land believed to be representative of that described by Fountain in 1885, where "thousands of tons of grama grass hay could be cut and baled." The dominant shrub is creosotebush.

plants, i.e., in seed coats, fruit coats, fruit pulp, endosperm, embryo, leaves, stems, roots, and bulbs. In some cases they are non-specific in their effects. Our tests were designed to determine the effects of aqueous extracts of creosotebush plant material on germination and growth of seedlings and established plants of creosotebush, black grama (*Bouteloua eriopoda* (Torr.) Torr.), and bush muhly (*Muhlenbergia porteri* Scribn.). Black grama and bush muhly are the major dominant species on creosotebush sites in the semidesert grassland.

LITERATURE REVIEW

The literature on growth inhibitors has been reviewed by Gray and Bonner (1948), Evenari (1949), and Bonner (1950). More recently, Muller (1953) found that both *Encelia* and *Franseria* leaves contain a water-soluble, toxic principle which effectively kills tomato seedlings in water culture, with *Franseria* the more potent of the two. Bennett and Bonner (1953) found marked responses in tomato plants subjected to aqueous extracts from several desert plants. The plants extracted, in order of severity of effects on the tomato plants, were *Thamnosma montana, Prosopis juliflora, Sarcobatus vermiculatus, Viguiera reticulata, Larrea tridentata, Encelia frutescens, Franseria dumosa, Chrysothamnus nauseosus, Dalea fremontii, Allenrolfea occidentalis,* and *Ephedra viridis.*

In the deserts of the Southwest it is common for certain species of plants to inhibit the growth of other plants in their immediate vicinity. This is true of *Encelia farinosa,* as shown by Gray and Bonner (1948). Went (1952) suggested that this phenomenon also applies to creosotebush and stated:

> After summer rains, it was observed that a large number of *Larrea* seedlings developed, partly under and partly between existing shrubs. A few weeks later, the seedlings under the old plants shriveled and died. This was not due to a lack of water, because all other young seedlings in that neighborhood remained perfectly healthy. A month later, all the *Larrea* seedlings about ½ meter away from the old plants had died too, and the radius of death progressed further and further until only the seedlings furtherest removed from any other existing shrub were left. Because of this *Larrea* plants are very regularly spaced, and the less frequent the rain the wider the spacing.

Again in 1955 he reported:

> The creosotebush is spread with amazingly even spacing over the desert; this is especially obvious from an airplane. The spacing apparently is due to the fact that the roots of the plant excrete substances which kill any seedlings that start near it. The distance of spacing is correlated with rainfall: the less rainfall the wider the spacing. This probably means that rain leaches the poisons from the soil so that they do not contaminate as wide an area.

This regular spacing of the creosotebush is not obvious on the mesas around Las Cruces; it is not unusual to find small creosotebush plants thriving directly under or within the canopy radius of larger creosotebush plants.

EXPERIMENTAL TESTS AND RESULTS

A preliminary germination test with creosotebush carpels, using separate extracts from creosotebush leaves, stems, and roots, indicated that the plant material did inhibit germination and that there was no apparent difference among the extracts obtained from the various plant parts. Test I was designed to study the effects of aqueous extracts of creosotebush carpels and a combination of creosotebush leaves and twigs on the germination and initial growth of black grama, bush muhly, and creosotebush. Test II was designed to study the effects of aqueous extracts of creosotebush plant material at concentrations likely to be found

under field conditions on the germination and initial growth of black grama, bush muhly, and creosotebush. Another objective of this test was to determine the effects of the osmotic concentrations of the extracts on germination and initial growth of those species.

Previous tests raised the question as to whether the creosotebush carpels might chemically inhibit germination of creosotebush seeds or structurally hinder germination. Therefore, test III determined the germination of creosotebush in the carpels; in seeds removed from the carpels but moistened with an extract made from the carpels; and in a solution of the same osmotic concentration as the carpel extract. Since previous tests indicated that creosotebush had slightly better germination under some moisture stress, test IV was designed to study the germination of creosotebush under various degrees of moisture stress.

General procedures

The extracts used in the various tests were obtained by finely chopping creosotebush plant material and soaking in tap water for a period of 48 hr. The liquid portion was used in the tests. All germination tests were made in petri dishes. All of the seeds used throughout this study were from the same lot. The creosotebush seeds were germinated at 17°C, which is below the optimum temperature for germinating creosotebush. However, total germination is obtained over a slightly longer period with a minimum growth of mold (Gerard 1959).[3] The grasses were germinated at 25°C.

Test I

Twenty-five seeds each of black grama, bush muhly, and creosotebush (removed from the carpels) were placed on doubled blotter paper in each of three petri dishes. Of the three dishes per species, one was treated with extract from creosotebush leaves and twigs; one was treated with extract from creosotebush carpels; and a control was treated with tap water. The extract from the leaves and stems was obtained by soaking 250 g of the material in 1 liter of water. The extract from the carpels was obtained by crushing 50 g of the material and soaking it in 250 ml of water. Determinations of pH were made by the potentiometric method. On the sixth day after the grasses began to germinate, and the twelfth day after creosotebush began to germinate, the plumules and radicles of each seedling were measured to determine differences in initial growth.

[3] Unpublished data, Animal Husbandry Dep., Agr. Exp. Sta., New Mexico State Univ., University Park, New Mexico.

Germination, initial growth, and pH levels obtained in test I are shown in Table I. The grass caryopses began to germinate after 24 hr, and germination was complete 48 hr after the test was initiated. The creosotebush seeds began to germinate on the third day after initiation, and none germinated after the ninth day. There was no apparent difference in the time required for germination of the seeds and caryopses treated with extract from creosotebush plant material, as compared to those treated with water. The radicle and plumule measurements shown in Table I were taken on bush muhly and black grama 7 days after the test was initiated and on creosotebush 15 days after the test was initiated.

The germination of black grama caryopses treated with the extract from creosotebush leaves and twigs was significantly lower than the other treatments (Table I). Germination of the other two species was not affected by the treatments. The radicle growth of both black grama and bush muhly was greatly reduced by both of the extracts. The plumule growth of black grama was also greatly reduced by both extract treatments, but only the extract from creosotebush leaves and twigs substantially reduced the plumule growth of bush muhly. The plumules and radicles of creosotebush were not greatly affected by the extract treatments. The carpel extract was less concentrated than the extract from the leaves and twigs, and the results were generally intermediate to those obtained with tap water and the extract from leaves and twigs.

TABLE I. Germination and initial growth of black grama and bush muhly (after 7 days) and creosotebush (after 15 days) treated with three different moistening agents

Species	Treatment[a]	pH	Germination (%)	Length of radicles (mm)	Length of plumules (mm)
Black grama	1	5.34	48.0	0.0	8.1
	2	6.11	76.0	5.0	7.8
	3	7.76	98.6	23.9	22.5
Bush muhly	1	5.34	95.3	0.0	6.0
	2	6.11	97.5	8.8	21.1
	3	7.76	98.6	28.9	33.6
Creosotebush	1	5.34	33.3	4.5	9.2
	2	6.11	36.0	6.9	9.0
	3	7.76	30.7	8.2	12.0
LSD (.05)			27.3	NS	NS

[a] Treatment 1 is extract from creosotebush leaves and twigs.
Treatment 2 is extract from creosotebush carpels.
Treatment 3 is tap water.

Test II

All of the mature leaves and approximately one-fourth of the twigs 6 inches and shorter were re-

TABLE II. Germination and initial growth of black grama, bush muhly, and creosotebush treated with three different concentrations of extract from creosotebush leaves and twigs and the three corresponding water-mannitol solutions

Species	Treatment[a]	Osmotic concentration (atm)	pH	Germination (%)	Length of radicles (mm)	Length of plumules (mm)
Black grama	1	3.50	5.71	80.0	0.0	10.0
	1A	3.50	—	90.0	18.5	23.2
	2	1.16	5.93	88.0	1.6	17.6
	2A	1.16	—	85.0	17.3	23.9
	3	1.29	6.09	94.0	7.6	23.1
	3A	1.29	—	89.0	19.6	24.2
LSD (.05)				NS	2.7	3.4
Bush muhly	1	3.50	5.71	94.0	0.0	9.5
	1A	3.50	—	95.0	10.3	25.5
	2	1.16	5.93	93.0	0.0	15.4
	2A	1.16	—	98.0	11.6	25.3
	3	1.29	6.09	96.0	0.0	15.5
	3A	1.29	—	99.0	11.3	26.4
LSD (.05)				NS	NA[b]	0.7
Creosotebush	1	3.50	5.71	65.0	—	—
	1A	3.50	—	66.0	—	—
	2	1.16	5.93	62.0	—	—
	2A	1.16	—	61.0	—	—
	3	1.29	6.09	54.0	—	—
	3A	1.29	—	57.0	—	—
LSD (.05)				NS		

[a]Treatment 1 is an extract from 134 g of creosotebush leaves and twigs; 1A is water-mannitol.
Treatment 2 is an extract from 67 g of creosotebush leaves and twigs; 2A is water-mannitol.
Treatment 3 is an extract from 33.5 g of creosotebush leaves and twigs; 3A is water-mannitol.
[b]Not analyzed

moved from an average creosotebush plant (3 ft 7 inches tall, 4 ft 3 inches canopy diameter). This material weighed 268 g. Extracts were prepared for treatments 1, 2, and 3 by soaking 134, 67, and 33.5 g, respectively, in 1,600 ml of tap water. We reasoned that should one-half of the leaves and one-eighth of the twigs fall from a plant during the course of one season, the amount of an inhibitory substance present in the soil would be comparable to that present in the treatment 1 extract. Treatments 2 and 3 were used to test the effects of a one-fourth and one-eighth leaf- and twig-fall. These extracts are probably less concentrated than might be expected to occur in the soil around a creosotebush plant where fallen leaves and twigs have accumulated over a period of time. This assumption is supported by Runyon (1934): "In the very driest seasons only buds and immature leaves remain on the plants and many twigs and older branches are almost invariably mulched with an accumulation of the dropped materials."

Six hundred seeds each of creosotebush (removed from the carpels), black grama, and bush muhly were placed on doubled blotter paper in petri dishes at the rate of 25 seeds per dish, making a total of 24 dishes per species. The six treatments were the three extracts described above and three water-mannitol solutions of the same osmotic concentrations as the creosotebush extracts. The osmotic concentrations were determined by the freezing-point-depression method. Mannitol, an inert electrolyte (Uhvits 1946), was used for preparing the solutions having the same osmotic concentrations as the three plant extracts. The amount of mannitol needed to prepare the solutions was calculated as described by Helmerick and Pfeifer (1954). Determinations of pH were made by the potentiometric method.

Ten milliliters of the appropriate agent were applied to each petri dish. Germination and growth of seedlings treated with each extract was compared with the results obtained from the appropriate water-mannitol solution. Germination counts were made daily. Six days after the grasses began to germinate, one replication of each treatment was randomly selected and the plumule and

radicle of each seedling was measured to determine differences in initial growth.

Table II gives the osmotic concentration of the treatments, the pH of the extracts, the germination percentage, and the initial growth for test II. The grass caryopses began to germinate after 24 hr, and germination was complete 48 hr after the test was initiated. The creosotebush seeds began to germinate on the second day after initiation, and none germinated after the seventh day. There was no apparent difference among treatments in the time required for germination of the grass caryopses. However, germination of creosotebush seeds in treatments 1 and 2 was delayed about 24 hr as compared to those treated with treatments 1A and 2A. The treatment 3 extract did not delay germination of creosotebush seeds. The various treatments did not significantly affect the total germination obtained within any of the species tested (Table II).

The radicle and plumule measurements for black grama and bush muhly (Table II) were taken 7 days after the test was initiated. The creosotebush seedlings were not measured because there was no apparent inhibitory affect on seedling growth. However, there were significant reductions in seedling growth of the grasses treated with the extracts, as compared to those treated with water-mannitol solutions of the same osmotic concentration as that of the extracts. The most striking response to treatment with the extracts was the reduction of, or complete inhibition of, radicle growth of the grasses. The black grama seedlings developed no radicles in the dishes treated with the strongest extract (treatment 1), and there was a significant reduction in the radicle growth in the dishes receiving treatments 2 and 3. None of the bush muhly seedlings treated with the creosotebush extracts developed radicles, and consequently the results were not statistically analyzed. The treatments 1 and 2 extract significantly reduced the growth of black grama plumules, but the treatment 3 extract did not significantly affect the plumule growth. All three of the plant extracts significantly reduced the plumule growth of bush muhly.

Fifteen days after initiation of the test, the plumules of the bush muhly seedlings had not made any appreciable growth over the previous observations. However, the plumules and radicles in the dishes treated with the water-mannitol solutions had attained lengths of 40 to 55 mm. Even after 15 days no radicles developed in the dishes treated with the creosotebush extracts.

The plumules of the black grama seedlings in treatments 1 and 2 grew in about the same pattern as the bush muhly seedlings. The effect of the extracts on the black grama radicles was not as marked as it was on those of bush muhly. However, no radicles developed with treatment 1, those that developed with treatment 2 all died by the 11th day, and those that developed with treatment 3 all died by the 16th day after initiation of the test. The radicles in the dishes treated with water-mannitol solutions appeared completely normal.

Higher concentrations of creosotebush plant extract (treatments 1 and 2) apparently affected the ability of creosotebush seedlings to survive. By the 23rd day after initiation of the test, 63.1% of the seedlings of treatment 1 had died while only 3.0% of the seedlings treated with 1A had died. The same general results were also found for the seedlings treated with 2 and 2A. However, there was no apparent difference in the mortality rates obtained for treatments 3 and 3A.

Test III

Five 1-inch squares of trebled blotter paper were arranged in each of eight petri dishes, and 400 creosotebush seeds (removed from the carpels) were placed on the squares at the rate of 10 seeds per square. Using the same technique, 200 carpels were placed in four petri dishes. These carpels were carefully chosen so that only large plump ones, likely to contain seeds, were used. The dishes containing the carpels were each watered with 10 ml of tap water, 2 ml for each square of blotter paper. Four of the dishes containing seeds (removed from the carpels) were treated with 10 ml of extract from the carpels from which they were removed. The extract was prepared by crushing the carpels and soaking them in 50 ml of water for 48 hr. The remaining four dishes of seeds were treated with a water-mannitol solution of the same osmotic concentration as that of the carpel extract. The technique of using the 1-inch squares of blotter paper served to concentrate the substrata around the seeds and carpels. Carpels treated with water were compared with seeds treated with carpel extract to determine whether carpels structurally inhibit germination. Seeds treated with carpel extract and water-mannitol solution were compared to determine whether the carpels contain a chemical inhibitor. The latter comparison is necessary to eliminate the possibility of a difference in germination due to differences in osmotic concentration. The osmotic concentration of the carpel extract was determined by the freezing-point-depression method. The amount of mannitol needed to prepare the solution was calculated as described by Helmerick and Pfeifer (1954).

The final germination percentages obtained in test III are shown in Table III. The osmotic

concentration of the carpel extract and the water-mannitol solution was 2.4 atm. There was no significant difference in germination of the seeds (removed from the carpels) treated with carpel extract and those treated with the water-mannitol solution; nor was lack of vigor apparent in the seedlings which developed under these conditions. Germination of seeds removed from the carpels was significantly greater than that of those not removed from the carpels. The germination of the seeds in the carpels was also greatly delayed as compared to the seeds of both treatments which were removed from the carpels.

TABLE III. Germination of creosotebush seeds not removed from the carpels and treated with tap water; creosotebush seeds removed from the carpels and treated with an extract from the carpels; and creosotebush seeds removed from the carpels and treated with a water-mannitol solution of the same osmotic concentration as that of the extract

Moistening agent	Seed condition	Percentage germination
Water	In the carpels	34.0 (after 60 days)
Carpel extract	Removed from the carpels	90.5 (after 9 days)
Water-mannitol solution	Removed from the carpels	89.5 (after 9 days)
LSD (.05)		6.5

Test IV

Four replications of 25 creosotebush seeds (removed from the carpels) each were treated with six water-mannitol solutions with osmotic concentrations of 0.33, 1.50, 2.40, 3.50, 5.00, and 7.00 atm. The 1.50-, 2.40-, and 3.50-atm osmotic concentration solutions were used because these are approximations of the osmotic concentrations of creosotebush extracts previously used. The 5.00- and 7.00-atm solutions were used to test the germination of the creosotebush under conditions of higher moisture stress.

Table IV. Germination of creosotebush seeds removed from the carpels when treated with six water-mannitol solutions of differing osmotic concentrations (degrees of moisture stress)

Osmotic concentration of water-mannitol solution (atm)	Percentage germination
0.33 (control)	66.0
1.50	47.0
2.40	50.0
3.50	45.0
5.00	46.0
7.00	33.0
LSD (.05)	18.3

All of the levels of moisture stress above field capacity (0.33 atm), except 2.40 atm, significantly reduced the germination of the creosotebush seeds (Table IV). However, the results among treatments with osmotic concentrations of 1.50 to 7.00 atm were non-significant (.05 level).

Other tests

To determine whether or not growing creosotebush plants exuded an inhibitor through the roots, established creosotebush plants (14–16 inches tall) with the soil removed from their roots were transplanted to pots with a gravel-sand substratum. Nutrient solution was recycled through the substratum for 37 days. Due to evapotranspiration, only 3% of the initial quantity of nutrient solution remained after the 29-day period. Black grama, bush muhly, and creosotebush were germinated in the concentrated recycled material and in tap water. The recycled material did not inhibit germination or initial growth of the species tested.

Several attempts to grow creosotebush from seed in pots in the greenhouse resulted in only small numbers surviving after 3 weeks. Most of the creosotebush seedlings perish during the first 15 days after emergence. This occurs before there can possibly be any contact of the roots among seedlings. The same high mortality among seedlings has been observed in the field. However, there is a very low mortality of seedlings that survive to an age of 3 weeks.

In a pot test, creosotebush extracts were applied to mature plants of black grama, bush muhly, and creosotebush. The extract was not detrimental to the treated plants. The plants treated with the extract, particularly the grasses, were obviously much more vigorous 10 days after treatment than were the controls. This increase in vigor appeared to be the result of the extract having sealed the soil surface in the pots, thereby reducing evaporation. The extract caused a crusting somewhat comparable to a thin film of asphalt. The fourth day after treatment all pots were watered with tap water, and the infiltration rate was much slower in the pots treated with extract than in the tap-water control pots. This effect may partially account for the poor infiltration characteristics of soils on creosotebush sites, and for the extreme deterioration of sites where creosotebush has become established.

DISCUSSION AND CONCLUSIONS

Aqueous extracts from creosotebush plant material, prepared in relatively high concentration (test I), significantly reduced the germination of black grama caryopses. The extracts used in test II,

possibly more comparable to field conditions, did not significantly reduce the germination of any of the species tested. However, the radicle growth of black grama and bush muhly was greatly reduced by even the least concentrated of the extracts. Plumule growth of black grama and bush muhly was also reduced by the extract treatments but not so drastically as the radicles. These reductions in initial growth apparently are the result of a water-soluble extract in the creosotebush plant material. Neither the relatively low osmotic concentrations nor the moderate pH's could account for the reduction in growth. Creosotebush germination and initial growth were relatively unaffected by the extracts used in tests I and II.

The results obtained in test III indicated that there is no water-soluble chemical substance present in the creosotebush carpels which inhibits the germination of creosotebush seeds. The delay in, and reduction of, germination of creosotebush seeds in carpels, as compared to those removed from the carpels, is apparently caused by a structural characteristic or a non-water-soluble chemical compound in the carpel itself.

Germinating creosotebush seeds under increased moisture stress reduced the germination percentage (test IV) though some earlier tests indicated that the opposite may occur.

Other results suggest that the creosotebush roots do not exude an inhibitory compound. Rather, there seems to be a high mortality from drought, heat, and diseases among young creosotebush seedlings.

The effects of the creosotebush extracts on initial growth of black grama and bush muhly plus the reduction in infiltration rate observed in potted soils treated with extracts could be contributing factors in the degeneration of grassland areas where creosotebush is invading.

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