# Effects of Aqueous *Artemisia* Extracts and Volatile Substances on Germination of Selected Species

G. R. HOFFMAN AND D. L. HAZLETT

**Highlight: The present study was done to determine the effects of *Artemisia* substances, both water-soluble and aromatic, on the germination of selected grassland species. Aqueous extracts of *Artemisia tridentata* litter inhibited germination of such species as *Agropyron smithii, Euphorbia podperae, Hedeoma hispida, Parietaria pennsylvanica,* and *Thlaspi arvense*. Aqueous extracts of *A. tridentata* and *A. cana* leaves inhibited germination of *Achillea millefolium, Artemisia cana, A. tridentata, Bromus inermis, Chrysothamnus nauseosus,* and *Thlaspi arvense*. Germination of these same six species was inhibited by volatile substances from leaves of *A. tridentata* and *A. cana*. Aqueous extracts of leaves of *Artemisia tridentata, A. cana, A. absinthium, A. frigida,* and *A. dracunculus* all inhibited germination of *Haplopappus spinulosus* and *Thlaspi arvense*. Germination of *Echinacea pallida* was inhibited by leaf extracts of all the *Artemisias* tested except *A. dracunculus*. Germination of *Plantago patagonica* was inhibited by leaf extracts of only *A. tridentata* and *A. dracunculus*. Germination of *Stipa viridula* and *S. comata* was stimulated by leaf extracts of *A. frigida* and *A. dracunculus*. Aqueous leaf extracts of *A. absinthium* strongly inhibited germination of *Stipa comata,* but stimulated germination of *Stipa viridula*. Germination of certain species, such as *Lepidium virginicum, Rumex crispus,* and *R. occidentalis,* were not at all inhibited by leaf extracts of any *Artemisias* tested. Results of this experiment suggest possible influences of *Artemisia* chemicals on species distributional patterns in *Artemisia*-dominated vegetation, though further studies are required to verify whether the influences are valid under field conditions.**

There has long been considerable interest in the toxic effects of plant extracts on other plants and the possible role of plant-plant interactions in the make-up of the plant community. In the case of *Artemisia* spp. early studies of Bode (1939) and Funke (1943) showed that *A. absinthium* leaves contained a substance which inhibited members of the genera *Levistium, Melissia,* and *Salvia;* but the same substance had no effect on *Stellaria* spp. Later observations on *A. absinthium* and *A. vulgaris* indicated allelopathic influences by both these species, but Grümmer (1961) suggested that lack of nitrogen in the soil could also explain the paucity of other plants near these *Artemisias*. In a laboratory study Jameson (1961) observed that both water and alcoholic extracts of *A. tridentata* inhibited somewhat the radical growth of wheat seedlings. Muller (1966) reported that volatile terpenes from both *A. tridentata* and *A. californica* inhibited germination and seedling growth of several herbaceous species under laboratory conditions. Muller (1966) also indicated that allelopathy may be a predominant influence in *A. tridentata*-dominated vegetation of the Great Basin, though no experimental data were presented. In a greenhouse study Schlatterer and Tisdale (1969) found that water leachates of *A. tridentata* litter retarded the germination and early growth of *Stipa thurberiana, Sitanion hystrix,* and *Agropyron spicatum*. After 4 weeks these grasses outgrew the controls, a result attributed to higher nitrogen content of the litter treatments. Reid (1964) reported the presence of water soluble inhibitor(s) in leaves of *A. tridentata, A. cana, A. tripartata,* and *A. nova* which under laboratory conditions inhibited germination and growth of *Bromus inermis, Sitanion hystrix,* and *Agropyron trachycaulum* as well as several other plants including radish, wheat, barley, and beans.

In an earlier paper we described spatial distributions of plant species within 6 × 6 m plots of *Artemisia tridentata*- and *A. cana*-dominated vegetation in western North Dakota (Hazlett and Hoffman 1975). We found that some species including *Parietaria pennsylvanica, Hedeoma hispida, Descurainia pinnata,* and *Euphorbia podperae* were more abundant under or near the *Artemisia* shrubs and grasses *Agropyron smithii, Bouteloua gracilis,* and *Stipa viridula* were more abundant in the spaces between the *Artemisia* shrubs. Although certain

Authors are professor of biology and research assistant, Department of Biology, University of South Dakota, Vermillion, South Dakota 57069.

Manuscript received August 4, 1976.

species appeared to be attracted to and other repelled by the *Artemisia* shrubs, the mechanism was not suggested by our data (Hazlett and Hoffman 1975).

The present study was done to test the effects of water-soluble leachates and aromatic compounds from *Artemisias* collected from western North Dakota on the germination of selected species under laboratory conditions.

## Methods

*Artemisia* foliage and litter samples were collected from *A. tridentata;* and foliage samples were collected from *A. cana, A. absinthium, A. frigida,* and *A. dracunculus*. All samples were collected from Theodore Roosevelt National Park, North Dakota, in or near the habitats of our earlier study (Hazlett and Hoffman 1975). From the same area we collected disseminules of species to be tested for germination responses.

*Artemisia* foliage was collected from the end decimeter of five branches from each of 10 shrubs of each species. Foliage samples were placed in paper sacks and air dried in the field. Litter samples were taken from directly under, or very near, 10 *A. tridentata* shrubs. It was not possible to collect all litter in the same stage of decomposition, and our samples had some relatively fresh litter as well as some very decomposed litter. Litter samples were also placed in paper sacks and air dried in the field. All foliage and litter samples were collected in late August; the disseminules of the test species were collected as they matured throughout the growing season. We were careful not to winnow disseminules in the field so as to lose adhering fruit materials. Specimens of all plants used in this study were collected for positive identification and then deposited in the University of South Dakota herbarium. All disseminules of species that were stratified were placed in petri dishes, moistened, then put in a refrigerator at 4°C for 60 days; 40 disseminules were placed in each petri dish.

### First Experiment

This experiment tested the effects of *Artemisia tridentata* litter extracts on the germination of selected species. The 10 litter samples were bulked into a single large sample. Litter extracts were made by soaking 1 g litter in 5 ml deionized water for 48 hours at 21°C. The extracts were then filtered through two layers of Whatman #1 filter paper and the filtrate stored in airtight bottles at 4°C until used. All extracts were made at the same time, and no more than 2 days passed before they were used. We tested germination responses of both stratified and unstratified disseminules. Sufficient disseminules were stratified to provide six dishes of 40 disseminules each of each species. Following stratification, we pipetted 2 ml litter extract into each of two dishes of each species, 5 ml litter extract into each of two more dishes of each species, and 2 ml additional deionized water into the remaining two dishes of each species, which served as controls. For unstratified disseminules we placed 2 ml litter extract in each of two dishes of each species. We set up two additional dishes of 40 unstratified disseminules each of each species for controls. All dishes were then placed in a growth chamber programmed for 16 hours light (1,000 ft-c) at 21°C and 8 hours dark at 10°C. Germination records were kept for 15 days following the extract additions.

### Second Experiment

This experiment was set up to test the effects of aqueous extracts of *A. tridentata* and *A. cana* leaves and the effects of aromatic compounds from these species on germination of selected species. Leaf extracts were made using 5 g air dry leaves/100 ml deionized water for 48 hours at 21°C. The extracts were then filtered through 2 discs of Whatman #1 filter paper and the filtrate stored in airtight bottles at 4°C until used. As in the first experiment, no more than 2 days passed before the extracts were used. Part of the extracts was diluted to ½ strength and part diluted to ¼ strength. We pipetted 1 ml of each extract concentration into each dish of disseminules to be tested. Treatments were done in duplicate. To test the effects of aromatic compounds of the *Artemisias*, we placed 5 g crushed *Artemisia* leaves in a 2,840-cc glass container along with two uncovered petri dishes containing disseminules of a given test species. The chambers were covered with glass plates sealed on with petrolatum. A sepa chamber was set up for each species tested. One of the petri dishes removed after 4 days and germination counted; the second was removed after 8 days and germination counted. In this experin test cultures were also placed in growth control chambers a experiment one.

### Third Experiment

The third experiment was done to test the relative effects of aque leaf extracts of *Artemisia tridentata, A. cana, A. absinthium, frigida,* and *A. dracunculus* on germination of selected species. leaf extracts were made using 2.5 g air dry leaves/100 ml deioni water. The extracts were made and filtered as before and stored a the previous experiments. After the 60-day stratification period, added 1 ml leaf extract to each dish such that each dish of dissemin received 1 ml of one of the *Artemisia* extracts; the sixth dish contai only deionized water and served as a control. Dishes were place growth control chambers as in the previous experiments. Germina records were kept for 15 days following stratification and ext additions.

## Results and Discussion

Results of experiment one, the effects of aqueous li extracts on germination, are given in Table 1. As sho *Artemisia tridentata* litter extracts inhibited the germinatio *Achillea millefolium, Agropyron smithii, Hedeoma hispi Parietaria pennsylvanica, Thlaspi arvense,* and possibly *P tago elongata* and *Euphorbia podperae*. There was no inhibi effect on the other species tested. Except for *Thlaspi Chrysothamnus* all species tested in this experiment occu vegetation in western North Dakota that is dominated *Artemisia tridentata*. In fact *Parietaria pennsylvanica, He oma hispida, Achillea millefolium,* and *Euphorbia podperae* all very abundant directly under the *Artemisia* shrubs (Haz and Hoffman 1975).

In experiment two all concentrations of leaf extracts of t *Artemisia tridentata* and *A. cana* inhibited germination of species tested. Results are given in Table 2; the degree inhibition was related to the concentrations of the extracts v least inhibition occurring in the least concentrated extra *Thlaspi arvense* and *Achillea millefolium* were most sensitiv *Artemisia* leaf extracts, though *A. tridentata* was also q sensitive. *Bromus inermis* was more sensitive to extracts of *cana* than *A. tridentata*. *B. inermis* is not an important specie

**Table 1. The percentage germination[1] of selected species exposed to a ous extracts of *Artemisia tridentata* litter.**

| Species tested | Disseminules stratified | | | Unstratified | |
|---|---|---|---|---|---|
| | Litter extract (2 ml) | Litter extract (5 ml) | Control | Litter extract (2 ml) | Contr |
| *Achillea millefolium* | — | — | 93 | 63 | 93 |
| *Agropyron smithii*[2] | 3 | 3 | 15 | 0 | 0 |
| *Allium textile* | 25 | 17 | 23 | 0 | 0 |
| *Artemisia cana* | — | 75 | 80 | 75 | 83 |
| *Artemisia tridentata* | 95 | 90 | 93 | 80 | 75 |
| *Chrysothamnus nauseosus* | 77 | 70 | 76 | 75 | 60 |
| *Euphorbia podperae*[2] | 10 | 8 | 17 | 0 | 0 |
| *Hedeoma hispida*[2] | 12 | 14 | 23 | 5 | 15 |
| *Orthocarpus luteus* | 80 | 60 | 65 | 0 | 0 |
| *Parietaria pennsylvanica*[2] | 40 | 42 | 80 | 0 | 0 |
| *Plantago elongata* | 23 | 27 | 33 | 15 | 23 |
| *Thlaspi arvense* | 37 | 33 | 50 | 25 | 50 |
| *Tragopogon dubius* | 7 | 3 | 5 | 0 | 0 |

[1]Counted after 15 days.

[2]These species all began germination at the 4°C stratification temperature before tr ments of extracts and aromatics were given. The percentages for these species in the t have been corrected for germination prior to treatments.

**Table 2. Percentage germination of selected species exposed to aqueous leaf extracts and aromatic compounds of *A. tridentata* and *A. cana*.**

| Species tested | Days after start | Concentrations of leaf extracts (grams air dry leaves/100 ml water) | | | | | | Exposure time (days) to aromatic compounds | | | | Control |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *A. tridentata* | | | *A. cana* | | | *A. tridentata* | | *A. cana* | | |
| | | 5.00 | 2.50 | 1.25 | 5.00 | 2.50 | 1.25 | 4 | 8 | 4 | 8 | |
| *Achillea millefolium* | 4 | 0 | 0 | 15 | 0 | 0 | 23 | 22[1] | — | 33[1] | — | 87 |
| | 8 | 0 | 33 | 79 | 0 | 0 | 65 | 72 | 40 | 47 | 43 | 97 |
| *Artemisia cana* | 4 | 3 | 9 | 22 | 0 | 7 | 41 | 27[1] | — | 40[1] | — | 77 |
| | 8 | 29 | 28 | 53 | 14 | 50 | 81 | 45 | 46 | 47 | 40 | 88 |
| *Artemisia tridentata* | 4 | 0 | 4 | 13 | 0 | 0 | 4 | 0[1] | — | 11[1] | — | 35 |
| | 8 | 0 | 16 | 25 | 4 | 11 | 29 | 35 | 17 | 33 | 27 | 52 |
| *Bromus inermis* | 4 | 0 | 3 | 3 | 0 | 9 | 9 | 46[1] | — | 33[1] | — | 46 |
| | 8 | 7 | 36 | 74 | 0 | 28 | 48 | 100 | 71 | 88 | 54 | 96 |
| *Chrysothamnus nauseosus* | 4 | 7 | 39 | 44 | 22 | 27 | 52 | 44[1] | — | 61[1] | — | 68 |
| | 8 | 37 | 39 | 45 | 42 | 46 | 61 | 93 | 68 | 64 | 61 | 72 |
| *Thlaspi arvense* | 4 | 0 | 0 | 19 | 0 | 0 | 0 | 3[1] | — | 0[1] | — | 8 |
| | 8 | 0 | 0 | 66 | 0 | 0 | 48 | 29 | 23 | 24 | 16 | 80 |
| *Raphanus sativus* | 4 | 23 | 29 | 69 | 0 | 28 | 54 | 38[1] | — | 46[1] | — | 85 |
| | 8 | 36 | 67 | 94 | 6 | 72 | 86 | 72 | 75 | 68 | 86 | 99 |

[1]These cultures were removed from the aromatic chambers after 4 days, then recounted after 8 days.

*A. tridentata* or *A. cana* dominated vegetation of western North Dakota. Reid (1964) also found *A. tridentata* leaf extracts inhibited germination of *B. inermis* in laboratory experiments. *Chrysothamnus nauseosus* was inhibited by extracts of *A. tridentata* and to a lesser extent by extracts of *A. cana*.

It is noteworthy that in most cases germination percentages did increase from the 4-day to the 8-day counts, indicating some initial retardation but not complete suppression of germination. Carley and Watson (1968) reported total inhibition of *Raphanus* germination by *A. tridentata* leaf extracts after 5 days, but their extracts were about three times more concentrated than our most concentrated one.

It is very difficult to know how much water soluble toxic material is leached from *Artemisia* foliage during a rainstorm or over an entire year. Some of this toxic material may be adsorbed onto clay colloids in the soil, some may be altered by microorganisms to reduce its toxicity. Additionally, it is very difficult to estimate the volatile chemical content in the air around the *Artemisias* and how this varies with time of day, windspeed, and season of the year. So the concentrations of water soluble extracts from *Artemisia* leaves as well as the concentrations of the volatile substances used in our experiments were arbitrary. For leaf extracts we used 2.5 g or 5 g air-dry leaves/100 ml water. The latter was also diluted 2 and 4 times. Carley and Watson (1968) used 5 g dry *Artemisia tridentata* leaves/35 ml water in their experiments; Muller and Muller (1956) used 10 g dry *Franseria dumosa* or *Encelia farinosa* leaves/100 ml water in their experiments. Chou and Muller (1972) used aqueous extracts of *Arctostaphylos glandulosa* plant parts ranging from 1 g dry plant material/99 ml water to 5 g dry plant material/95 ml water. In our experiments dealing with aromatic compounds of *Artemisia* we used 5 g dry leaves/2,840 cc volume. In a typical experiment involving *Salvia leucophylla* aromatic terpenes, Muller (1965) used a ratio of leaf material to volume of .125 g/500 cc. This is about 1/7 the ratio of *Artemisia* leaves/volume used in our experiments. Muller (1965) reported complete inhibition of germination of *Bromus rigidus* and *Festuca megalura* under these conditions, but using *Cucumus sativus* as a test species, germination and seedling growth occurred even in the presence of 2 g *Salvia* leaves in a 500 cc volume.

Aromatic compounds from leaves of both *Artemisia tridentata* and *A. cana* suppressed germination of *Achillea millefolium, Artemisia tridentata, A. cana, Thlaspi arvense,* and to a lesser degree *Chrysothamnus nauseosus* and *Raphanus sativa*. As shown in Table 2, germination in most cases was less after 8 days exposure than after 4 days exposure followed by 4 days out of the chambers. *Raphanus sativus* was one exception that germinated somewhat better after 8 days exposure to either *A. tridentata* or *A. cana* aromatics. *A. cana* germinated slightly better when exposed to 8 days in the *A. tridentata* chamber. The marked improvement in germination during the 4 days out of the chambers indicated the species recovered rather quickly from the suppression of germination. *Chrysothamnus nauseosus* germinated 61% during the 4 days in the *A. cana* chamber and only an additional 3% during the 4 days out of the chamber. Only *Bromus inermis* and *Chrysothamnus nauseosus* germinated to a greater extent than their respective controls (Table 2). Since *Achillea* occurs near and directly under *A. tridentata* shrubs, aromatic inhibition very likely is ineffective for this species in western North Dakota. Also, the concentration of aromatic compounds of our laboratory experiment undoubtedly exceeded that occurring in the field at any one time. *Agropyron smithii* and *Chrysothamnus nauseosus* are more abundant away from the *Artemisia* shrubs, and germination of *Chrysothamnus* was not inhibited by aromatic compounds from *Artemisia* leaves (Table 2).

Results of the third experiment are shown in Table 3. This experiment was done to show the relative effects of aqueous extracts of five different species of *Artemisia* on the germination of selected species. The 18 species tested all occur in western North Dakota, but not all occur in vegetation types with the *Artemisias* used in this experiment (Hazlett and Hoffman 1975). As shown in Table 3, not all *Artemisia* extracts have the same influence on the germination of the test species. *Echinacea pallida* was inhibited by all extracts except that of *A. dracunculus,* while *Plantago patagonica* was inhibited by extracts of *A. tridentata* and *A. dracunculus* but not by the remaining three species extracts. *Stipa comata* was strongly inhibited by *A. absinthium* extract but germinated better in extracts of *A. frigida* and *A. dracunculus* than in the control. *Elymus canadensis* was inhibited by *A. cana* extract, but in *A. tridentata* and *A. frigida* extracts, it germinated more than in control cultures. *Ratibida columnifera* was inhibited only by *A. tridentata* extracts. Some species, like *Rumex crispus, R. occidentalis, Lepidium virginicum, Stipa spartea, S. comata, S. viridula,* and *Oenothera biennis,* all germinated quite well with or without the addition of

**Table 3. Percentage germination[1] of 18 species tested against leaf extracts of five *Artemisia* species. Test species were collected in western North Dakota within or close to habitat in whivh the *Artemisias* occurred.**

| Test species | Leaf extracts of | | | | | Controls | |
|---|---|---|---|---|---|---|---|
| | *A. tridentata* | *A. cana* | *A. absinthium* | *A. frigida* | *A. dracunculus* | Stratified | Unstratified |
| *Artemisia absinthium* | 55 | — | — | — | — | 47 | 0 |
| *Artemisia cana* | 100 | — | — | — | — | 80 | 77 |
| *Artemisia dracunculus* | 0 | — | — | — | — | 5 | 0 |
| *Artemisia frigida* | 10 | — | — | — | — | 13 | 0 |
| *Bromus inermis* | 97 | — | — | — | — | 100 | 100 |
| *Echinacea pallida* | 7 | 5 | 7 | 5 | 15 | 17 | 3 |
| *Elymus canadensis* | 47 | 17 | 30 | 50 | — | 33 | 30 |
| *Haplopappus spinulosus* | 0 | 3 | 5 | 3 | — | 20 | 0 |
| *Lepidium virginicum* | 95 | 100 | 97 | 97 | — | 100 | 0 |
| *Oenothera biennis* | 77 | 77 | 83 | 75 | 73 | 75 | 7 |
| *Plantago patagonica* | 5 | 27 | 30 | 15 | 5 | 20 | 10 |
| *Ratibida columnifera* | 10 | 23 | 27 | 23 | — | 25 | 0 |
| *Rumex crispus* | — | 73 | 65 | 70 | 63 | 85 | 80 |
| *Rumex occidentalis* | — | 93 | 95 | 90 | 85 | 80 | 5 |
| *Stipa comata* | 11 | 10 | 3 | 23 | 25 | 10 | 5 |
| *Stipa spartea* | 11 | 13 | 15 | 13 | 17 | 13 | 3 |
| *Stipa viridula* | 35 | 30 | 45 | 43 | 57 | 37 | 20 |
| *Thlaspi arvense* | — | 20 | 33 | 25 | 23 | 95 | 80 |

[1]Counted after 15 days.

*Artemisia* extracts. *S. comata* showed some inhibition by *A. absinthium* extract, though in *A. dracunculus* and *A. frigida* extracts it germinated considerably better than in control cultures. Neither *Rumex* occurs in *Artemisia*-dominated vegetation in western North Dakota, though *Lepidium, Oenothera,* and *Stipa* all do. *Haplopappus spinulosus* and *Thlaspi arvense* germinated uniformly poorly, or not at all, in all *Artemisia* extracts.

Results of these experiments suggest possible plant-plant interactions that might occur in nature. However, conclusive statements must await further studies done under carefully controlled conditions in the field. It could be significant, for example, that *Bromus inermis* and *Chrysothamnus nauseosus* germination was inhibited by *Artemisia* extracts and that neither species occurred in stands of *Artemisia*-dominated vegetation of western North Dakota (Hazlett and Hoffman 1975). *Agropyron smithii* was also inhibited by *Artemisia* extracts and it occurs most abundantly in *Artemisia*-dominated vegetation of western North Dakota in the spaces between the dominant shrubs. Not all examples of germination inhibition under laboratory conditions can be supported by correspondingly favorable observation in the field. In our experiments the germination of *Parietaria pennsylvanica, Euphorbia podperae, Hedeoma hispida,* and *Achillea millefolium* was inhibited by litter extracts of *Artemisia tridentata*. Yet, in the field, these same species are most abundant directly under or very near *A. tridentata* shrubs. It is possible that species sensitive to *A. tridentata* litter germinate in the litter only when sufficient precipitation has reduced the levels of the inhibiting substance(s). Microbial decomposition may also play an important role in decomposing inhibitory substances. Additionally, it is possible that species insensitive to the *A. tridentata* litter might germinate in the moist litter only to die from desiccation before their radicles reach moisture in the mineral soil. These are suggestions that could help explain results of this experimental study that seem contradictory to earlier field observations (Hazlett and Hoffman 1975).

It is important to point out that most plant-plant interactions are not simple one factor interactions. A plant is influenced by a multiplicity of environmental factors, chemical inhibition being only one of many. As Muller (1970) indicated, one can point to phytotoxins as controlling species distributions only after careful and systematic testing of other biotic and abiotic factors of the environment which potentially influence plant distribution. Even then a limiting factor operates in the natural environment with other factors which may not be limiting in the strict sense of the word, but could still augment the effects of the factor considered to be limiting.

## Literature Cited


**Bode, H. R. 1939.** Uber die Blattausscheidungen des Wermuts und ihre Wirkung auf andere Pflanzen. Planta 30:567-589.

**Carley, H. E., and R. D. Watson. 1968.** Effect of various aqueous plant extracts upon seed germination. Bot. Gaz. 129:57-62.

**Chou, C., and C. H. Muller. 1972.** Allelopathic mechanisms of *Arctostaphylos glandulosa* var. *zacaensis*. Amer. Midl. Nat. 88:324-347.

**Funke, G. 1943.** The influence of *Artemisia absinthium* on neighboring plants. Blumea 5:281-293.

**Grümmer, G. 1961.** The role of toxic substances in the interrelationships between higher plants. p. 219-228. *In:* F. L. Milthorpe (Ed.), Mechanisms in Biological Competition. Academic Press Inc., New York.

**Hazlett, D. L., and G. R. Hoffman. 1975.** Plant species distributional patterns in *Artemisia tridentata*- and *Artemisia cana*-dominated vegetation in western North Dakota. Bot. Gaz. 136:72-77.

**Jameson, D. A. 1961.** Growth inhibitors in native plants of northern Arizona. U.S. Forest Service, Rocky Mountain Forest and Range Exp. Sta. Res. Note No. 61, 2 p.

**Muller, C. H. 1965.** Inhibitory terpenes volatilized from *Salvia* shrubs. Bull. Torrey Bot. Club 92:38-45.

**Muller, C. H. 1966.** The role of chemical inhibition (allelopathy) in vegetational composition. Bull. Torrey Bot. Club 93:332-351.

**Muller, C. H. 1970.** The role of allelopathy in the evolution of vegetation. p. 13-31. *In:* K. L. Chambers (Ed.) Biochem. Evolution, Proc. 29th Ann. Biol. Colloq., Oregon State Univ. Press, Corvallis.

**Muller, W. H., and C. H. Muller. 1956.** Association patterns involving desert plants that contain toxic products. Amer. J. Bot. 43:354-361.

**Reid, A. 1964.** Growth inhibitors in shrub species in Wyoming. Bull. Ecol. Soc. Amer. 45:94. (abstr.)

**Schlatterer, E. F., and E. W. Tisdale. 1969.** Effects of litter of *Artemisia, Chrysothamnus,* and *Tortula* on germination and growth of three perennial grasses. Ecology 50:869-873.