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ECOLOGICAL STUDIES ON PLANT INHIBITION BY <u>SOLANUM ROSTRATUM</u>

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INTRODUCTION

The action of plant inhibitors is frequently manifested by growth repression or total absence of the sensitive species in the presence of the inhibitor-producing plants (Bonner 1950, Garb 1961). These inhibitors may be produced by the roots as recent studies with brome grass (Benedict 1941), guayule (Bonner and Galston 1944, Bonner 1946), and horseweed (Keever 1950) have shown. The sunflower stem (Curtis and Cottam 1950), the potato tuber (Hemberg 1947, 1954), the cocklebur stem (Khudairi and Bonde 1954), and the quackgrass rhizome (Hamilton and Buchholtz 1955) are examples of stems which have exhibited the production of inhibitors. An inhibitor is produced by the leaves of *Artemisia* and reaches the ground through leaching of the living leaves by rain (Bode 1939, Funke 1943). Similar areas of production have been noted in *Encelia* (Gray and Bonner 1948), *Franseria* (Muller 1953), and cocklebur (Bonde and Khudairi 1954,

Khudairi and Bonde 1954). In the former species the inhibitor remains in the leaves as they are shed at the base of the plant and is leached into the soil by seasonal rains.

Inhibitors are not confined to the vegetative organs but also occur in the reproductive organs, such as the seeds of beet (Funke 1941), wheat (Barton and Solt 1948), cabbage, lettuce, and sunflower (Evenari 1949). The fruits of oats (Ruge 1939, Stout and Tolman 1941, and Elliott and Leopold 1953), cocklebur (Khudairi and Bonde 1954), and sugar beet (Duym et al. 1947) also produce inhibitors affecting the germination and growth of other species.

Among the many methods used to assay quantitatively the growth substances produced by plants is the coleoptile section test (Bonner 1933, 1946, Bentley and Housley 1954). In most studies the sections are floated on the test solutions or immersed therein. Germination tests are sometimes used for a quantitative assay of growth inhibitors (Evenari 1949). The results are usually expressed as average root length per unit time or percentage germination.

The extent to which inhibitors determine ecological phenomena, such as the composition of a plant community or the sequence of particular species in a successional pattern, is of great importance. Studies with Encelia (Went 1942,

Gray and Bonner 1948) and with Artemisia (Funke 1943) suggest that plant inhibitors may be important in determining the floristic composition of areas surrounding these plants. Inhibiting effects of brome grass (Benedict 1941), sunflower (Curtis and Cottam 1950), horseweed (Keever 1950), and desert plants (Muller and Muller 1956) have been suggested as being ecologically important in interspecies competition and successional trends.

The primary goals of the present investigation were to determine whether early invaders in abandoned fields in central Oklahoma produce substances which are inhibitory to other seed plants, and to study the possible role of such inhibitors in succession.

METHODS AND MATERIALS

In preliminary tests tomato plants (Lycopersicum esculentum var. "Marglobe"[1]) were used as the test species, and were grown in water extracts of seven invader species; wiregrass (Aristida oligantha), Japanese brome (Bromus japonicus), sandbur (Cenchrus pauciflorus), lambs-quarters (Chenopodium album), annual sunflower (Helianthus annuus), foxtail grass (Setaria viridis), and buffalo-bur (Solanum rostratum). The method of growth employed was that of Bonner and Galston (1944) with some modifications. Using ten replications the results indicated that the extracts of Japanese brome and buffalo-bur were most inhibitory with the death of seven assay plants in the extract of the former species and all the test plants in the latter species.

Interest was stimulated in further experimentation with buffalo-bur, since it is rarely important in early

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[1]Scientific nomenclature of the forbs follows that of Fernald (1950), and of the grasses that of Hitchcock and Chase (1950).

successional stages for more than one consecutive year in a given plot. More thorough studies were made subsequently with buffalo-bur to determine: (1) the location of the inhibitor in the plant, (2) the effect of the inhibitor on germination and growth of the test species (tomato) and on some species which are competitors of buffalo-bur, (3) the amount of the inhibitor present using the Avena coleoptile section test, and (4) the possible ecological implications of the inhibitor in soil and sand from the standpoint of germination, growth and development, competition, and decomposition.

A reliable and convenient assay method proposed by Bonner and Galston (1944) was used to determine the exact location of the production of the inhibitor in buffalo-bur and its subsequent effect on growth. Twelve-day old tomato seedlings of uniform size grown in sand culture were selected as the assay plants. The seedlings were transplanted to 35 ml vials containing the test solutions. These solutions contained various proportions of Hoagland and Arnon's (1938) No. 2 nutrient solution mixed with water extracts of buffalo-bur plant material. The water extracts in the preliminary experiment were prepared by using 10 g of plant material per 100 ml of distilled water. Since all plants died in this extract concentration, the inhibitory activity was reduced

by cutting the total amount of plant material used in all later studies. Thus, water extracts of six parts of the buffalo-bur plants: (1) roots, (2) stems, (3) immature leaves (less than 1-inch long), (4) mature leaves (over 2-inches long), (5) seeds, and (6) fruit coats were prepared by using 5 g of plant material per 100 ml of distilled water. Fresh weights were used for all vegetative organs, whereas the weights of the reproductive organs were based upon material collected and stored about a year prior to usage. Extractions were made by chopping the material in a Waring blender for 5 minutes and filtering with a Buchner funnel. Three series were tested each with different concentrations of the extract as follows: (1) 30 ml of extract, (2) 15 ml of extract with 15 ml of nutrient solution, (3) 5 ml of extract with 25 ml of nutrient solution. The control series contained 30 ml of nutrient solution only. Five assay plants were tested in each concentration of extract and the control. The vials were covered with aluminum foil to prevent decomposition of the test solutions by light. A small hole in the foil served for introduction of the assay plants into the test solutions and stabilization of the plants. The plants were grown under greenhouse conditions for 7 days, after which they were removed from the vials, and oven-dried

at 95 C for 48 hours. The dry weights of the plants were recorded for statistical analyses. The inhibitory activity of buffalo-bur on competitor species was determined by repeating the above test using 12-day old wiregrass, Japanese brome, or buffalo-bur plants as the assay species.

Extracts were prepared from fresh and air-dried (90 days) whole plants of buffalo-bur as described above to test the stability of the inhibitor. These extracts were boiled for five minutes. The control extracts received no heating. Dilutions of the extracts and assay of the activity of the inhibitor were repeated as set out above using tomato as the assay species.

The effect of microbial activity on the extract or on the assay species was tested by filtering mature leaf extract prepared as stated above through a Morton bacteriological filter. The roots of two tomato and two buffalo-bur plants (12-day old) were sterilized in a 0.1% solution of mercuric chloride and the plants were inserted into sterile, aluminum-covered 35 ml vials containing the sterile test solutions. Sterile cotton was used to cover the position of plant insertion through the foil. Assay of the inhibitor was repeated as described previously.

Tests were also made to determine whether a reduction

in water absorption by the roots of the assay plants grown in the most concentrated extracts might effect growth inhibition. Twelve-day old tomato plants were grown in dilutions of 0.5 M calcium chloride stock solution (Machlis and Torrey 1956). The dilution which had an osmotic pressure high enough to retard water absorption by the tomato roots was applied to epidermal tissue of Rheo discolor. It was possible to ascertain if an osmotic effect was operative by comparing the percentage of cells plasmolyzed by this dilution of calcium chloride and the concentrated extracts of the six plant parts of buffalo-bur.

The inhibitory activity of buffalo-bur on germination was tested by germinating the seeds of tomato in Petri dishes on filter paper moistened by the test solutions (Stout and Tolman 1941). Extracts of the six plant parts were prepared as previously described. The test solutions were prepared by dilution of the extracts with distilled water. Three series were tested each with different concentrations of the extract as follows: (1) 10 ml of extract, (2) 5 ml of extract with 5 ml of distilled water, (3) 2 ml of extract with 8 ml of distilled water. The control series contained 10 ml of distilled water only. The series was duplicated for each concentration of the extract and the control. The

Petri dishes were covered and placed in the dark for 14 days. They were then removed and the number of seeds germinated in each dish and the lengths of the radicles (Konis 1947) of the seedlings were recorded for statistical analysis. The above test was repeated with wiregrass, Japanese brome, and buffalo-bur as the assay species. However, the radicle length was not recorded for these three latter species. The use of the buffalo-bur seeds in this test was impractical because it was difficult to create conditions under which the control seeds reached even 40% to 50% germination. This test was repeated in duplicate for all species.

A quantitative assay of the inhibitor was obtained by means of the oat coleoptile section test. Assay plants (Avena sativa var. "Victory") were grown in quartz sand according to the methods described by Larsen (1955). Coleoptile sections 10 mm in length were cut by a specially constructed cutter with double blades. Ten sections were transferred to each Petri dish containing 10 ml of the test solution. These solutions were prepared by diluting the extracts of the six plant parts of buffalo-bur with a 10 mg per liter solution of indoleacetic acid (IAA). Since growth inhibition might be caused by supra-optimal concentrations of auxin (Larsen 1955), the growth-inducing activity of IAA

on the oat sections was determined as a control. Four series were tested each with different concentrations of the extract as follows: (1) 10 ml of extract, (2) 9.9 ml of extract with 0.1 ml of the IAA solution, (3) 5.0 ml of extract with 5.0 ml of IAA, (4) 1.0 ml of extract with 9.0 ml of IAA. The control series utilized 10 ml of the IAA solution only. Ten coleoptile sections were placed in each concentration of the extract and the control. A series was run also using similar ~~di~~so lutions of distilled water and the IAA solution. The oat sections were allowed to grow in the dilutions for 24 hours in the dark at 25 C. Images of the sections magnified four times with a photographic enlarger were then measured (Bentley and Housley 1954). This experiment was repeated three times and the results were averaged.

The effect of decomposing buffalo-bur shoots and roots upon the germination and growth of tomato plants was tested in quartz sand and soil. These cultures were prepared by mixing 80 g of air-dry shoots or roots of buffalo-bur per 4,000 g of planting medium. Four-inch glazed crocks were used as containers in the quartz sand studies. One series consisted of four pots containing decomposing shoots of buffalo-bur and a second series consisted of four pots containing decomposing roots. Two control pots without

decaying material were prepared also. Twenty-five tomato seeds were planted per crock for the germination tests. Two other series of pots were prepared with the same number of replications. Three, 12-day old tomato plants were transplanted into each crock of this group. The plants were watered periodically with nutrient solution. Leachate was held to a minimum. After growth under these conditions in the greenhouse for 30 days, the plants were harvested. The roots were separated from the shoots, both parts were dried at 95 C for 48 hours, and the oven-dry weights were recorded for statistical analysis. This test was repeated three times using the same planting medium for all three trials without any further addition of buffalo-bur material. The entire experiment was repeated three times in soil culture using 4-inch clay pots. The plants were irrigated periodically with cistern water. The growth and germination of buffalo-bur itself was tested in sand and soil culture only with decomposing buffalo-bur shoots because little root material was available. Germination of the seeds of this species was so poor that the results were not included in this study. Only one trial was run for buffalo-bur as the assay species.

The interaction of living tomato and buffalo-bur plants was studied by transplanting 12-day old seedlings of

the two species together in sand culture. Four series of 4-inch glazed crocks were prepared with 10 pots in each series: (1) two buffalo-bur plants, one tomato plant, (2) three tomato plants, (3) two buffalo-bur plants, one tomato plant, and (4) three buffalo-bur plants. The crocks were irrigated twice weekly with nutrient solution and at all other times when necessary with distilled water. Leachate from the crocks was collected and returned to the pots after watering. The plants were grown under greenhouse conditions. Flower buds were removed as formed from half of the buffalo-bur plants. All plants were then harvested, the roots were separated from the shoots, both parts were dried at 95 C for 48 hours, and the oven-dry weights were recorded for statistical analysis. A new series of plants was then transplanted into the same pots without changing the potting medium. The study was repeated three times, but only the data for the last two trials were recorded. Visual differences in growth were so slight in the first trial between the test series and the controls that oven-dry weights of the plants were not determined. The tomato plants in the first trial were transplanted into the test crocks 1 week prior to the buffalo-bur seedlings. Because visual differences were negligible as stated above, the buffalo-bur plants were transplanted into

the test crocks 1 week prior to the tomato seedlings in the second trial. It was hoped that this action might compensate for the faster rate of growth of the tomato plants. The seedlings of both species were transplanted into the test crocks at the same time in the third trial.

RESULTS

Of the vegetative organs the immature leaf extracts caused the greatest inhibition of tomato plants (Table I). The root extracts had the least effect on the growth of the tomato seedlings. In the case of the reproductive organs, the fruit extracts had a greater inhibitory effect on tomato seedlings than the seed extracts. The inhibition of the tomato seedlings by leaf extracts was statistically significant in all dilutions, but for the roots and stems only the two most concentrated solutions of the extract significantly affected the growth of tomato plants. The inhibition caused by the vegetative organs cannot be compared with that caused by the reproductive organs inasmuch as fresh weights were used in calculating the concentrations of the extracts of the vegetative organs and air-dry weights in the case of the reproductive organs. The mean oven-dry weights were nearly the same for seedlings grown in the most concentrated solutions of the extracts of the seeds and fruits. The results indicated that with greater dilution of the extract the

differences in weights of plants grown in extracts of seeds and fruits became greater. This phenomenon might be explained by the counteraction between inhibitors and auxins produced in the seed. Because the seed and fruit extracts showed inhibitory action for all dilutions, it appeared that the auxins produced by the embryo were not sufficient to completely offset the effects of the inhibitors.

All extracts of fresh and air-dry buffalo-bur showed significant inhibition over the controls (Table II). It was also found that heating either the fresh or air-dry material had no significant effect on the inhibitory action of the extract on the growth of tomato plants when the mean oven-dry weights of the plants grown under these two conditions were compared with one another. When the mean oven-dry weights of the tomato plants grown in heated extracts were compared with those of plants grown in extracts without heating, it was found that a slight loss of inhibitory activity occurred due to heating. Apparently some alteration of the inhibitor occurred through heating but not enough to eliminate total inhibitory activity.

Sterilized tomato and buffalo-bur seedlings grown in mature leaf extract which had been passed through a bacteriological filter were significantly inhibited in growth. This

appears to eliminate the possibility that growth inhibition was due to microbial activity in the extract.

In experiments concerned with the possible role of plasmolysis in the inhibitory action of the extract, it was found that at least a 0.1M solution of calcium chloride was necessary to cause tomato plants to wilt. This solution caused plasmolysis of 90% to 100% of the epidermal cells of Rheo discolor. When the most concentrated extracts of the various plant organs of buffalo-bur were tested on the epidermal cells of Rheo discolor, no plasmolysis of the cells occurred. Thus, it would appear that the osmotic pressure of the extracts was not the cause of the inhibition of growth of tomato seedlings.

Wiregrass seedlings were definitely inhibited in growth by extracts of buffalo-bur and, of all vegetative organs, the extracts of mature leaves were most inhibitory (Table III). The root and stem extracts were least effective in inhibition. Retardation of growth of wiregrass in extracts of mature and immature buffalo-bur leaves was statistically significant in all dilutions. The most concentrated root and stem extracts also effected significant inhibition of growth of wiregrass. The fruit extracts were slightly more inhibitory to wiregrass than the seed extracts.

Extracts of both reproductive organs caused statistically significant inhibition of the assay species in all dilutions.

Japanese brome seedlings were inhibited in growth by extracts of buffalo-bur and, of all vegetative organs, the extracts of immature leaves were most inhibitory (Table IV). The root extracts were least effective in growth inhibition of this test species. Inhibition of growth of this species was statistically significant in all dilutions of the vegetative organs, with the exception of the least concentrated solutions of the immature and mature leaves. It should be noted that with greater dilution of the root extracts, more inhibition of Japanese brome growth was found. The same phenomenon occurred in the fruit extracts. The reason for this increase in inhibitory activity with greater dilution of the extract was not clear. The seed extracts caused a greater inhibition of growth of the assay species than the fruit extracts at higher concentrations. The Japanese brome seedlings in the least concentrated solutions had a significant increase in growth compared with the controls. Seedlings in the most concentrated solutions were significantly inhibited in growth, however. The significant increase in growth of Japanese brome in the least concentrated solutions of the seed extracts may have been due to a counteraction of

the inhibitors in the seeds by auxins produced in the embryo. Perhaps native auxins were also responsible for the increase of growth of the test species in fruit extracts.

Extracts of buffalo-bur were inhibitory to the growth of seedlings of its own species. Of vegetative organs, the stem extracts caused the greatest inhibition of growth of this test species. Inhibition of growth in the most concentrated extracts of the roots, stems, and mature leaves was statistically significant. Growth of buffalo-bur seedlings was significantly inhibited in the extract solutions of the intermediate concentrations for immature leaves, but no significant inhibition was found in the strongest concentration of the extract. This may be explained by the fact that growth in this species was highly variable. The seed extracts were more effective in growth inhibition of buffalo-bur than the fruit extracts. The extracts of both reproductive organs caused significant inhibition of growth except for the weakest solution of the fruit extract.

Tests for inhibitory activity of buffalo-bur extracts on seeds of tomato indicated that, of the extracts of vegetative organs, the immature leaf extracts most effectively retarded germination of the seeds (Table VI). Inhibition of germination was statistically significant in the

weakest concentration of the immature leaf extracts. Inhibition by extracts of seeds was greater than those of fruits. The inhibition of germination in the most concentrated solution of seed extracts was statistically significant.

The length of the radicles of tomato seeds germinated and grown in extracts of buffalo-bur demonstrated the possible action of an inhibitor in these extracts (Table VII). The roots in these solutions were shriveled, twisted, and dark brown in color. The formation of secondary roots was scant, but many adventitious roots were formed above the radicle. The inhibition of growth of the radicles was statistically significant in the two most concentrated solutions of the extracts.

There was significant inhibition of germination of wiregrass seeds compared with the controls in only the two most concentrated solutions of the fruit extracts (Table VII). The possible reason for inadequate results with this species could have been the poor germination of the seeds on filter paper. Significant inhibition of germination of Japanese brome was noted in the most concentrated solutions of seed and fruit extracts (Table VII). Germination of buffalo-bur seeds on filter paper saturated with its own extracts was so poor that the results were not included.

The immature leaf extracts were most effective in inhibiting the growth of oat coleoptile sections (Table VIII and Figure 1). The stem extracts, of all the vegetative organs, seemed to have the least inhibitory activity. The fruit extracts were more inhibitory than the seed extracts. Reductions in growth in length of the oat coleoptiles in all extract dilutions for both vegetative and reproductive organs were statistically significant. It was possible from Figure 1 to obtain an estimate of the amount of inhibitor contained in each plant organ in terms of IAA units. By observing the graph for distilled water and its points of intersection with the line graphs for the various extract solutions, the quantity of inhibitor sufficient to counteract the amount of IAA in the extract at that point could be determined. It was found that 1 g fresh weight of root material contained enough inhibitor to counteract the effect of 38.8 μg of IAA. Sufficient inhibitor was located in 1 g fresh weight of stem material to counteract the effect of 16.8 μg of IAA. The effect of 82.7 μg of IAA was counteracted by the amount of inhibitor contained in 1 g fresh weight of immature leaves. Sufficient inhibitor was contained in 1 g fresh weight of mature leaves to counteract the effect of 49.2 μg of IAA. The effect of 8.9 μg of IAA was counteracted by the amount of inhibitor

contained in 1 g of air-dry seed material. Sufficient inhibitor was found in 1 g of air-dry fruit material to counteract the effect of 41.0 μg of IAA.

There was no apparent statistically significant effect of decomposing parts of buffalo-bur plants on tomato plants grown in sand (Table IX). The significant increase in the development of shoots of tomato plants grown in decomposing buffalo-bur shoots may be due to an abundance of nutrients released by the decomposition of organic material. The loss of dry weights of the tomato plants in the second and third trials in both decomposing shoots and roots may be due to an accumulation of nutrients because the pots were not leached with distilled water at any time.

A significant inhibition in growth of the roots of tomato plants occurred when grown in decomposing shoots and roots of buffalo-bur plants in soil during the first trial subsequent to the addition of the buffalo-bur material (Table X). No significant differences were noted in growth of the tomato plants in decomposing material in the second trial. Both the roots and shoots of tomato plants grown in decomposing shoots and roots of buffalo-bur showed a significant increase in growth over the controls in the third trial. Buffalo-bur material was added only before the first

trial. Apparently an inhibitor was released from the buffalo-bur in the early stages of decomposition, and it had disappeared by the time the second crop of tomatoes was planted. During the third trial a stimulation of growth in the test plants over the control plants might be indicative of an accumulation of available minerals in the soil as a result of decomposition.

The roots and shoots of buffalo-bur grown in soil with decomposing shoots of its own species were significantly inhibited in growth in comparison with the control plants (Table XI). No inhibition in growth of buffalo-bur was noted in the sand cultures.

The germination of tomato seeds was significantly inhibited in sand containing decomposing shoots of buffalo-bur. This inhibition was significant for all three trials. No significant inhibition in germination of tomato seeds was noted in sand cultures containing decomposing root material. These data do not agree with the findings concerning a lack of inhibition of growth in tomato seedlings grown in decomposing material in sand culture (Table X), but the inhibitor may be more critical in its effect on the germination of tomato seeds than on subsequent growth. Significant inhibition occurred in the germination of tomato seeds in soil

containing either decomposing shoots or roots in the first trial. No inhibition of germination was noted in successive trials when no new buffalo-bur material was added. This seemed to substantiate the findings recorded in Table X in which the inhibitor was operative in the first trial but apparently became inactivated prior to later trials.

When two buffalo-bur plants were grown in sand culture with one tomato plant no visual differences between the test plants and the control plants of either species were noted in the first trial (Tables XIII and XIV). Therefore, the oven-dry weights of the plants were not recorded. In the second trial (in the same pots and sand without leaching) a significant increase in growth of the shoots and roots of buffalo-bur occurred when grown with one tomato plant (Table XIII). No statistically significant differences in growth of the buffalo-bur plants were found in the third trial in comparison with the control plants. A marked decline in the oven-dry weights and appearance of all buffalo-bur plants occurred from the first to the third trials. This suggested that they were producing substances which were quite inhibitory to their own growth. No significant differences in growth were noted by the removal of the reproductive buds from half of the buffalo-bur plants.

In the second trial a statistically significant inhibition in growth of the tomato plants occurred when grown with buffalo-bur plants (Table XIV). No significant inhibition was noted in the third trial. The oven-dry weights of the tomato plants grown with buffalo-bur increased from the second to the third trial even though the control tomato plants showed a slight decline in growth from the first to the third trial. This was probably because the buffalo-bur plants grew very poorly in the third trial, thus competing less with the tomato plants.

DISCUSSION

The question of whether or not buffalo-bur plants produced an inhibitory growth substance was clearly settled in the studies with tomato plants and oat coleoptile sections. Experimentation with wiregrass, Japanese brome, and buffalo-bur seedlings grown in extracts of various organs of buffalo-bur indicated that the inhibitor may be active on buffalo-bur itself as well as on species with which it competes under field conditions. Benedict (1941) and Keever (1950) reported that brome grass and horseweed respectively were inhibitory to their own species. Bonner (1946) reported inhibition of guayule seedlings by the parent plants, Curtis and Cottam (1950) suggested this same phenomenon on field observations of prairie sunflower, and Went (1955) stated a similar finding in studies with evergreen creosote bush. On the other hand Gray and Bonner (1948) stated that no such inhibition of its own species occurs in Encelia.

The studies also indicated that the sensitivities of different species to the extracts of various organs of

buffalo-bur differed considerably. Garb (1961) reported a high degree of selectivity of various inhibitors for the sensitive species. In this project, extracts of the shoots apparently effected greater inhibition of all species tested than did extracts of the roots. Ether extracts of unexpanded leaves of cocklebur showed more inhibitory activity than the fully expanded leaves and the greatest inhibition of any plant part when tested on tomato (Khudairi and Bonde 1954). This fact was noted in the present study for water extracts of buffalo-bur tested upon tomato plants. Studies on oat coleoptiles grown in various organ extracts of buffalo-bur indicated that the place of greatest production of the inhibitor was in the immature leaves with the least amount occurring in the stems. On the other hand, the stem extracts of buffalo-bur were most inhibitory to the growth of buffalo-bur plants. This may be an indication of differences in sensitivity or it may result from the fact that the period of the year for the tests and perhaps the test materials were not the same. Thus, the inhibitor may move from one area of the plant to another or may not be produced in equal quantities in a given area at all times.

The evidence gathered in this study indicated that no appreciable inactivation of the inhibitor took place by

allowing the buffalo-bur plant material to air-dry. However, boiling the various extracts significantly reduced the inhibitory activity. Mergen (1959) found that in Ailanthus leaves there was a loss of inhibitory activity after boiling the extracts.

The extracts of buffalo-bur not only affected the growth of various species, but also had some inhibitory effects on the germination of seeds of competitor species and tomato. No prolongation of the period of germination was noted due to the extracts. Ovesnov and Shchekina (1960) stated that extracts of the subterranean parts of creeping couch grass, thistle, and sow thistle possessed substances which reduced germination and prolonged the period of germination. Nielsen et al. (1960) reported that alfalfa extract was very active in inhibiting germination of six species tested. The present study indicated that, of the vegetative organs, extracts of the leaves most effectively reduced the percentage of germination for both tomato and Japanese brome. Funke (1943) reported that extracts of fresh leaves of sage reduced the percentage of germination of seeds of a number of species.

The inhibitor was shown to occur as a possible root exudate in studies with buffalo-bur and tomato plants growing

together in the same pots of sand. In the first trial when the tomato plants were transplanted prior to those of buffalo-bur no inhibition of growth of the tomato plants occurred. It may be that the tomato plants increased in stature and competitive power considerably before the effect of the inhibitor became prominent, or it may be that an insufficient amount of the inhibitor was formed to retard growth of the tomato plants. In the second trial (using the same unleached sand) in which the buffalo-bur plants were transplanted prior to the tomato plants there was an increase in growth of the buffalo-bur plants in pots with one tomato plant compared with the controls with three buffalo-bur plants. Brenchley (1919) emphasized that the total weight of five plants in one pot is about the same as that of one plant in a pot. Growth seems to be proportional to the amount of minerals in the soil. Thus, it seemed possible that the decrease in growth of the three buffalo-bur plants in the same pot compared with growth in pots containing two buffalo-bur plants and one tomato plant was due to a greater amount of inhibitor being present in the sand and not to competition. Inhibition of the tomato plants apparently occurred in the pots with the buffalo-bur plants for these plants were smaller than the control tomato plants. Considering the general

decline of all plants from the first to the third trial, it seemed possible that the inhibitor produced by the roots was operative throughout the three trials. It may be that in sand culture the microflora was inadequate to reduce or eliminate the effect of the inhibitor. This evidence apparently confirmed the results of Went (1942) concerning the production of a chemical inhibitor by living plants, but it was contrary to the evidence found in the study of Keever (1950) with horseweed in which only the decomposition material produced effective inhibitors.

The germination of tomato seeds in decomposing buffalo-bur material indicated no prolongation of the period of germination. There was a decrease in percentage germination of tomato seeds in decomposing buffalo-bur material in soil and sand. Hamilton and Buchholtz (1955) found a delay in the germination of weedy species in cultures containing non-living quackgrass rhizomes. Gray and Bonner (1948) reported that rain may leach the inhibitory substance from fallen leaves and result in inhibition of germination of seeds around the inhibitor-producing plant.

Production or the release of the inhibitor was found to occur as a result of the decomposition of buffalo-bur material in soil but not in sand. Keever (1950) found that

a retardation in growth of horseweed occurred due to the decomposition of horseweed in the soil. The results of this study seemed to substantiate this premise. The results also agreed with Keever's findings that plants grown in sand containing decaying organic matter to which nutrient solution had been added were not inhibited in growth.

The ineffectiveness of the inhibitor in the decomposition material in soil after 30 days may have been due to several factors. Bonner (1946) reported that the inhibitor in guayule may have been rapidly destroyed by the soil microflora, and Gray and Bonner (1948) reported a similar situation for the inhibitor produced by Encelia. Börner (1960) demonstrated that micro-organisms decompose non-toxic excretions which in turn release phyto-inhibitors. Muller and Muller (1956) suggested that the inactivation of the inhibitors may be due to microbial activity, adsorption on soil colloids, or instability under xeric conditions.

The inhibitor in the decomposing material seemed to be most effective initially in the stunting of root growth. This type of effect could also have been brought about by root exudates acting on living plants. Perhaps decomposition of dead buffalo-bur plants and the production of root exudates by living plants under field conditions creates an

unfavorable environment which has an inhibitory effect on the germination and growth of that species as well as associated species even though the soil has sufficient moisture and nutrients for growth of most of the plants. It is doubtful if any one factor is the primary cause of floristic composition or successional trends. The complexity of the plant community may be at least partially the result of toxins produced by some plants and toxin tolerance by other plants (Muller and Muller 1956). The evidence was good in these studies that the inhibitor in buffalo-bur was operative in both soil and sand. This may be ecologically important in that only a few species, including itself, are found growing in close proximity to buffalo-bur plants, and this species is virtually replaced by its competitors after the first year of growth. Thus, the production of an inhibitor by buffalo-bur plants could be one of the factors determining vegetational change and the trend of successional stages in abandoned fields in central Oklahoma.

SUMMARY

Substances were produced by buffalo-bur plants which inhibited the germination and growth of that species as well as plants of other species. Extracts of the buffalo-bur leaves apparently caused the greatest inhibition of the vegetative organs. It was difficult to determine whether the extracts of seeds were more inhibitory than those of fruits. Variations in responses of various test species to the extracts of buffalo-bur were encountered. The part of the buffalo-bur plant effecting the greatest inhibition of the susceptible plant also varied with the species tested.

The inhibitor could be extracted with water from fresh or air-dry material. It could also be reduced in activity by boiling the extracts.

A quantitative assay of the inhibitor by means of the oat coleoptile section test revealed that 1 g of plant material contained sufficient inhibitor to counteract the growth-stimulating effect of 8.9 μg to 82.7 μg of indoleacetic acid, the amount depending on the organ from which

the extract was obtained. Extracts of immature leaves gave the greatest inhibition of the assay species in this test.

Decomposition products of buffalo-bur shoots and roots in soil inhibited the growth of tomato and buffalo-bur plants. The inhibitor was short-lived in soil and it is possible that it was destroyed quickly by the microflora in the soil. No inhibition due to decomposition products was noted in sand.

Inhibitors from decomposition products were more active in reducing the germination of certain seeds tested than on the subsequent growth and development of the same seedlings in sand and soil.

Growth-inhibiting substances were apparently released by living buffalo-bur plants as root exudates and retarded the growth of tomato and buffalo-bur plants in sand cultures.

It appears probable that both living buffalo-bur plants and the decomposition products of these plants could directly affect the floristic composition or the trend of succession in abandoned fields.

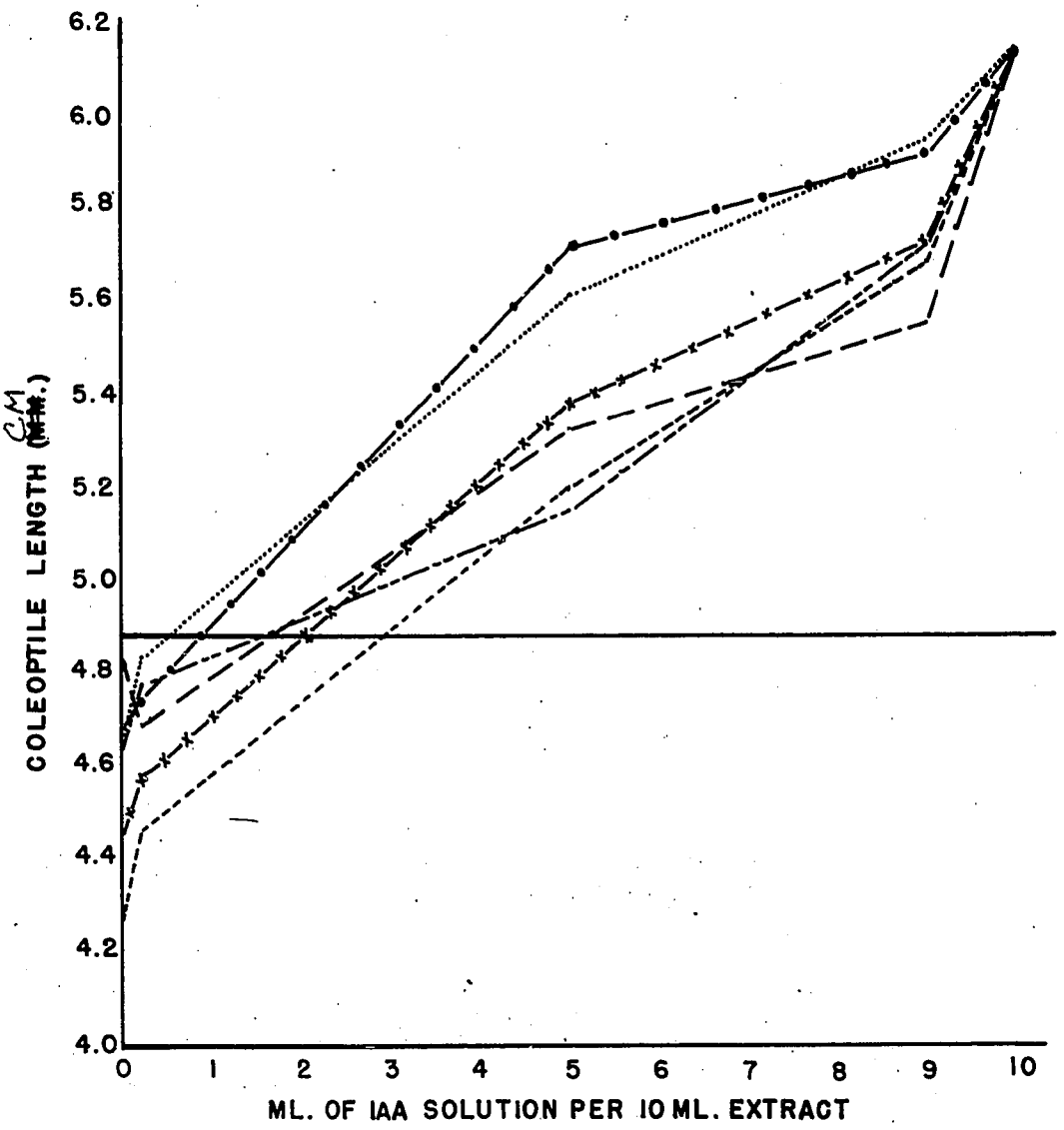

Fig. 1. Effect of water extracts of various plant organs of Solanum rostratum diluted with 0.1% solution of IAA on the growth in length of Avena coleoptile sections. The graph for growth in length of sections in distilled water is also shown. The symbol legend is as follows:

— — — — Root Extract

· · · · · · · · Seed Extract

—·—·—·— Stem Extract

---------- Fruit Extract

-------- Immature Leaf Extract

———— Distilled Water

-x-x-x-x- Mature Leaf Extract

Table I. Mean oven-dry weights (with SE) of 12-day old tomato plants (g) grown in water extracts of Solanum rostratum for 7 days.

Type of Extract	Treatment (ml)			
	30E/ON**	15E/15N	5E/25N	OE/30N
Roots	$0.0086 \pm 14.9 \times 10^{-8}$*	$0.0174 \pm 466.1 \times 10^{-8}$*	$0.0236 \pm 178.4 \times 10^{-8}$	
Stems	$0.0072 \pm 125.6 \times 10^{-8}$*	$0.0129 \pm 346.8 \times 10^{-8}$*	$0.0224 \pm 412.7 \times 10^{-8}$	
Immature Leaves	$0.0032 \pm 16.9 \times 10^{-8}$*	$0.0044 \pm 132.8 \times 10^{-8}$*	$0.0113 \pm 149.6 \times 10^{-8}$*	
Mature Leaves	$0.0045 \pm 17.0 \times 10^{-8}$*	$0.0044 \pm 78.6 \times 10^{-8}$*	$0.0135 \pm 147.4 \times 10^{-8}$*	
Seeds	$0.0027 \pm 1.3 \times 10^{-8}$*	$0.0047 \pm 18.5 \times 10^{-8}$*	$0.0091 \pm 122.0 \times 10^{-8}$*	
Fruits	$0.0029 \pm 33.4 \times 10^{-8}$*	$0.0033 \pm 92.8 \times 10^{-8}$*	$0.0062 \pm 97.9 \times 10^{-8}$*	
Control				$0.0264 \pm 80.7 \times 10^{-8}$

*Difference between this value and control significant at 1% level.

**Proportion of extract, E, to nutrient solution, N.

Table II. Mean oven-dry weights (with SE) of 12-day old tomato plants (g) grown in water extracts of fresh and air-dry Solanum rostratum for 7 days.

Type of Extract	Treatment (ml)			
	30E/ON**	15E/15N	5E/25N	OE/30N
Fresh Material (No Heat)	$0.0066 \pm 7.5\times10^{-8}$*	$0.0051 \pm 9.5\times10^{-8}$*	$0.0113 \pm 125.5\times10^{-8}$*	
Fresh Material (Boiled 5 min.)	$0.0048 \pm 10.0\times10^{-8}$*	$0.0058 \pm 8.5\times10^{-8}$*	$0.0105 \pm 17.5\times10^{-8}$*	
Air-Dry Material (No Heat)	$0.0068 \pm 41.0\times10^{-8}$*	$0.0054 \pm 22.5\times10^{-8}$*	$0.0116 \pm 31.0\times10^{-8}$*	
Air-Dry Material (Boiled 5 min.)	$0.0040 \pm 10.0\times10^{-8}$*	$0.0051 \pm 2.0\times10^{-8}$*	$0.0100 \pm 19.0\times10^{-8}$*	
Control				$0.0122 \pm 249.5\times10^{-8}$

*Difference between this value and corresponding one for control plants significant at 1% level.

**Symbols same as Table I.

Table III. Mean oven-dry weights (with SE) of 12-day old Aristida oligantha plants (g) grown in water extracts of Solanum rostratum for 7 days.

Type of Extract	Treatment (ml)			
	30E/ON/	15E/15N	5E/25N	OE/30N
Roots	$0.0051 \pm 55.7\times10^{-8}$**	$0.0046 \pm 85.0\times10^{-8}$**	$0.0080 \pm 128.5\times10^{-8}$	
Stems	$0.0050 \pm 87.5\times10^{-8}$**	$0.0068 \pm 60.4\times10^{-8}$	$0.0065 \pm 236.9\times10^{-8}$	
Immature Leaves	$0.0032 \pm 4.3\times10^{-8}$*	$0.0058 \pm 28.0\times10^{-8}$**	$0.0033 \pm 28.2\times10^{-8}$**	
Mature Leaves	$0.0027 \pm 49.4\times10^{-8}$*	$0.0025 \pm 7.7\times10^{-8}$*	$0.0029 \pm 12.4\times10^{-8}$*	
Seeds	$0.0047 \pm 49.4\times10^{-8}$*	$0.0033 \pm 2.1\times10^{-8}$*	$0.0027 \pm 3.4\times10^{-8}$*	
Fruits	$0.0033 \pm 17.5\times10^{-8}$*	$0.0032 \pm 14.4\times10^{-8}$*	$0.0026 \pm 36.1\times10^{-8}$*	
Control				$0.0094 \pm 118.6\times10^{-8}$

*Difference between this value and corresponding one for control plants significant at 1% level.

**Difference between this value and corresponding one for control plants significant at 2% level.

/Symbols same as Table I.

Table IV. Mean oven-dry weights (with SE) of 12-day old Bromus japonicus plants (g) grown in water extracts of Solanum rostratum for 7 days.

Type of Extract	Treatment (ml)			
	30E/ON**	15E/15N	5E/25N	OE/30N
Roots	$0.0023 \pm 10.6\times10^{-8}$	$0.0007 \pm 0.3\times10^{-8}$*	$0.0015 \pm 0.5\times10^{-8}$*	
Stems	$0.0010 \pm 12.2\times10^{-8}$*	$0.0013 \pm 0.6\times10^{-8}$*	$0.0014 \pm 3.1\times10^{-8}$*	
Immature Leaves	$0.0005 \pm 4.4\times10^{-8}$*	$0.0007 \pm 0.1\times10^{-8}$*	$0.0019 \pm 72.7\times10^{-8}$	
Mature Leaves	$0.0007 \pm 1.8\times10^{-8}$*	$0.0011 \pm 2.5\times10^{-8}$*	$0.0018 \pm 10.9\times10^{-8}$	
Seeds	$0.0018 \pm 10.4\times10^{-8}$	$0.0020 \pm 7.1\times10^{-8}$	$0.0065 \pm 15.2\times10^{-8}$*	
Fruits	$0.0047 \pm 5.8\times10^{-8}$*	$0.0034 \pm 1.6\times10^{-8}$	$0.0039 \pm 6.5\times10^{-8}$	
Control				$0.0029 \pm 14.7\times10^{-8}$

*Difference between this value and corresponding one for control plants significant at 1% level.

**Symbols same as Table I.

Table V. Mean oven-dry weights (with SE) of 12-day old Solanum rostratum plants (g) grown in water extracts of Solanum rostratum for 7 days.

Type of Extract	Treatment (ml)			
	30E/ON//	15E/15N	5E/25N	OE/30N
Roots	$0.0051 \pm 71.8\times10^{-8}$*	$0.0145 \pm 613.5\times10^{-8}$	$0.0145 \pm 326.9\times10^{-8}$	
Stems	$0.0047 \pm 46.6\times10^{-8}$*	$0.0074 \pm 251.5\times10^{-8}$	$0.0084 \pm 218.3\times10^{-8}$	
Immature Leaves	$0.0072 \pm 407.0\times10^{-8}$	$0.0073 \pm 15.8\times10^{-8}$/	$0.0099 \pm 328.0\times10^{-8}$	
Mature Leaves	$0.0055 \pm 16.9\times10^{-8}$*	$0.0090 \pm 235.5\times10^{-8}$	$0.0092 \pm 43.5\times10^{-8}$	
Seeds	$0.0045 \pm 31.9\times10^{-8}$*	$0.0046 \pm 19.6\times10^{-8}$*	$0.0066 \pm 22.1\times10^{-8}$/	
Fruits	$0.0059 \pm 64.7\times10^{-8}$**	$0.0063 \pm 13.7\times10^{-8}$**	$0.0092 \pm 136.4\times10^{-8}$	
Control				$0.0099 \pm 108.4\times10^{-8}$

*Difference between this value and corresponding one for control plants significant at 1% level.

**Difference between this value and corresponding one for control plants significant at 2% level.

/Difference between this value and corresponding one for control plants significant at 5% level.

//Symbols same as Table I.

Table VI. Germination of various seeds (with SE) on filter paper in 10 ml water extracts of Solanum rostratum.

Type of Extract		Number of Seeds Germinated per Species		
		Tomato	Aristida	Bromus
Roots	10E/0D//	9 ± 0	3 ± 0	7 ± 1
	5E/5D	8 ± 0	1 ± 0	8 ± 1
	2E/8D	8 ± 0	4 ± 0	9 ± 0
Stems	10E/0D	9 ± 1	1 ± 0	8 ± 2
	5E/5D	8 ± 0	2 ± 0	9 ± 1
	2E/8D	8 ± 0	3 ± 0	9 ± 0
Immature Leaves	10E/0D	2 ± 1**	3 ± 0	5 ± 1/
	5E/5D	8 ± 1	1 ± 1	6 ± 0
	2E/8D	9 ± 1	5 ± 0	9 ± 0
Mature Leaves	10E/0D	9 ± 0	3 ± 0	5 ± 0/
	5E/5D	9 ± 0	2 ± 1	8 ± 1
	2E/8D	9 ± 0	4 ± 2	8 ± 0
Seeds	10E/0D	4 ± 0/	1 ± 0	0 ± 0*
	5E/5D	8 ± 0	2 ± 0	1 ± 1*
	2E/8D	9 ± 0	2 ± 0	6 ± 1
Fruits	10E/0D	6 ± 4	0 ± 0/	0 ± 0*
	5E/5D	9 ± 0	2 ± 0	1 ± 1*
	2E/8D	9 ± 0	6 ± 1	6 ± 1
Controls	0E/10D	9 ± 0	5 ± 0	10 ± 0

*Difference between this value and corresponding one for control plants significant at 1% level.

**Difference between this value and corresponding one for control plants significant at 2% level.

/Difference between this value and corresponding one for control plants significant at 5% level.

//Proportion of extract, E, to distilled water, D.

Table VII. Growth of tomato seedlings (with SE) in water extracts of Solanum rostratum plants for 7 days.

	Treatment (ml)				
	10E/0D/	5E/5D	9E/1D	9.9E/0.1D	0E/10D
Length of Seedlings (cm)	10.05± 0.3527*	11.42± 0.2062**	12.12± 0.1887	12.38± 0.0687	13.57± 0.3947

*Difference between this value and corresponding one for control plants significant at 1% level.

**Difference between this value and corresponding one for control plants significant at 2% level.

/Symbols same as Table VI.

Table VIII. Measurements (with SE) of images of Avena coleoptile sections (1 cm) grown in water extracts of Solanum rostratum for 24 hours. Images magnified x 4 by enlarger.

Type of Extract	Treatment (ml)				
	10E/0IAA**	9.9E/0.1IAA	5E/5IAA	1E/9IAA	0E/10IAA
Roots	4.82± 0.0024*	4.69± 0.0030*	5.32± 0.0026*	5.55± 0.0016*	
Stems	4.68± 0.0013*	4.74± 0.0016*	5.71± 0.0052*	5.91± 0.0035	
Immature Leaves	4.26± 0.0013*	4.45± 0.0019*	5.19± 0.0017*	5.68± 0.0018*	
Mature Leaves	4.45± 0.0023*	4.57± 0.0043*	5.38± 0.0085*	5.73± 0.0039*	
Seeds	4.65± 0.0052*	4.83± 0.0029*	5.61± 0.0051*	5.94± 0.0055	
Fruits	4.64± 0.0010*	4.77± 0.0016*	5.15± 0.0015*	5.72± 0.0031*	
Controls					6.13± 0.0080

*Difference between this value and corresponding one for control plants significant at 1% level.

**Proportion of extract, E, to indoleacetic acid, IAA.

Table IX. Mean oven-dry weights (with SE) of tomato plants (g) grown in decomposing material of Solanum rostratum in sand for 30 days.

Trial	Plant Part	Treatment		
		Decomposing Shoots	Decomposing Roots	Controls
1	Shoots	3.16 ± 0.0299*	2.98 ± 0.0440	2.64 ± 0.0012
	Roots	1.87 ± 0.2422	1.06 ± 0.0751	1.34 ± 0.1640
2**	Shoots	3.05 ± 0.0364	2.87 ± 0.0137	3.10 ± 0.0003
	Roots	1.38 ± 0.1383	1.14 ± 0.0673	1.14 ± 0.0000
3**	Shoots	2.27 ± 0.0217	1.67 ± 0.0271	1.72 ± 0.0484
	Roots	0.86 ± 0.0346	0.49 ± 0.0058	0.79 ± 0.0930

*Difference between this value and corresponding one for control plants significant at 5% level.

**Grown in same pots as Trial 1 without any subsequent additions of Solanum rostratum.

Table X. Mean oven-dry weights (with SE) of tomato plants (g) grown in decomposing material of Solanum rostratum in soil for 30 days.

Trial	Plant Part	Treatment		
		Decomposing Shoots	Decomposing Roots	Controls
1	Shoots	3.81 ± 0.2733	3.06 ± 0.0587	3.46 ± 0.0182
	Roots	1.99 ± 0.1305*	2.15 ± 0.2570**	3.99 ± 0.0006
2/	Shoots	3.25 ± 0.0737	2.52 ± 0.0401	2.47 ± 0.2862
	Roots	1.22 ± 0.0275	1.02 ± 0.0120	0.81 ± 0.0441
3/	Shoots	1.90 ± 0.0127*	0.98 ± 0.0086**	0.56 ± 0.0081
	Roots	0.76 ± 0.0158*	0.20 ± 0.0002**	0.15 ± 0.0000

*Difference between this value and corresponding one for control plants significant at 1% level.

**Difference between this value and corresponding one for control plants significant at 5% level.

/Grown in same pots as Trial 1 without any subsequent additions of Solanum rostratum.

Table XI. Mean oven-dry weights (with SE) of Solanum rostratum plants (g) grown in decomposing shoots of Solanum rostratum in sand and soil for 30 days.

Substrate	Treatment			
	Shoots		Controls	
	Shoots	Roots	Shoots	Roots
Sand	0.86 ± 0.0600	0.39 ± 0.0289	1.42 ± 0.0498	0.75 ± 0.0751
Soil	0.41 ± 0.0030*	0.11 ± 0.0009*	0.77 ± 0.0068	0.45 ± 0.0102

*Difference between this value and corresponding one for control plants significant at 5% level.

Table XII. Mean number (with SE) of tomato plants germinating in decomposing material of Solanum rostratum.

Trial	Treatment					
	Decomposing Shoots		Decomposing Roots		Controls	
	Sand	Soil	Sand	Soil	Sand	Soil
1	14 ± 1.25*	19 ± 0.17**	20 ± 0.25	17 ± 0.92**	22 ± 1.00	22 ± 0.50
2	15 ± 1.83**	18 ± 2.25	20 ± 0.58	17 ± 1.33	22 ± 2.00	19 ± 4.00
3	12 ± 3.92*	19 ± 1.25	14 ± 0.25/	19 ± 3.08	22 ± 0.00	21 ± 1.00

*Difference between this value and corresponding one for control plants significant at 1% level.

**Difference between this value and corresponding one for control plants significant at 5% level.

/Evidence is that this value is erroneous due to damping off of seedlings.

Table XIII. Mean oven-dry weights (with SE) of 2 Solanum rostratum plants (g) grown in sand culture with 1 tomato plant.

Trial/	Plant Part	Treatment	
		Flowers	No Flowers
2	Shoots	8.02 ± 0.1165*	7.86 ± 0.1531*
	Roots	1.09 ± 0.0043**	1.22 ± 0.0110**
3	Shoots	0.73 ± 0.0231	0.92 ± 0.0364
	Roots	0.08 ± 0.0005	0.11 ± 0.0012
Controls - Three Solanum rostratum plants			
2	Shoots	3.98 ± 0.5387	5.03 ± 0.0581
	Roots	0.62 ± 0.0321	0.89 ± 0.0076
3	Shoots	0.87 ± 0.0051	0.96 ± 0.0163
	Roots	0.12 ± 0.0001	0.12 ± 0.0003

*Difference between this value and corresponding one for control plants significant at 1% level.

**Difference between this value and corresponding one for control plants significant at 5% level.

/Data not recorded for Trial 1.

Table XIV. Mean oven-dry weights (with SE) of 1 tomato plant (g) grown in sand culture with 2 Solanum rostratum plants.

Trial/	Plant Part	Treatment		
		Flowers**	No Flowers**	Control
2	Shoots	0.24 ± 0.0143*	0.19 ± 0.0033*	1.75 ± 0.0041
	Roots	0.10 ± 0.0015*	0.09 ± 0.0004*	0.49 ± 0.0019
3	Shoots	0.84 ± 0.0942	0.70 ± 0.0416	1.07 ± 0.0016
	Roots	0.16 ± 0.0031	0.16 ± 0.0019	0.19 ± 0.0005

*Difference between this value and corresponding one for control plants significant at 1% level.

**These are weights of tomato plants grown in cultures of Solanum rostratum with or without flowers.

/Data not recorded for Trial 1.

LITERATURE CITED

Barton, L. V., and M. L. Solt. 1948. Growth inhibitors in seeds. Contrib. Boyce Thompson Inst. 15: 259-278.

Benedict, H. M. 1941. The inhibitory effect of dead roots on the growth of bromegrass. J. Am. Soc. Agr. 33: 1108-1109.

Bentley, J. A., and S. Housley. 1954. Bio-assay of plant growth hormones. Physiol. Plant. 7: 405-419.

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

Bonde, E. K., and A. K. Khudairi. 1954. Further experiments with a growth inhibitor extracted from Xanthium leaves. Physiol. Plant. 7: 66-71.

Bonner, J. 1933. The action of the plant growth hormone. J. Gen. Physiol. 17: 63-76.

_____. 1946. Further investigation of toxic substances which arise from guayule plants: relation of toxic substances to the growth of guayule in soil. Botan. Gaz. 107: 343-351.

_____. 1950. The role of toxic substances in the interaction of higher plants. Botan. Rev. 16: 51-65.

Bonner, J., and A. W. Galston. 1944. Toxic substances from the culture media of guayule which may inhibit growth. Botan. Gaz. 106: 185-198.

Börner, H. 1960. Liberation of organic substances from higher plants and their role in the soil sickness problem. Botan. Rev. 26: 393-424.

Brenchley, W. E. 1919. Some factors in plant competition. Ann. Appl. Biol. 6: 142-170.

Curtis, J. T., and G. Cottam. 1950. Antibiotic and autotoxic effects in prairie sunflower. Bull. Torrey Botan. Club 77: 187-191.

Duym, C. P. A., J. G. Komen, A. J. Ultée, and B. M. Von der Weide. 1947. The inhibition of germination caused by extracts of seed balls of the sugar beet (Beta vulgaris). Proc. Kon. Ned. Akad. Wet. Amsterdam. 50: 527-535.

Elliott, B. B., and A. C. Leopold. 1953. An inhibitor of germination and of amylase activity in oat seeds. Physiol. Plant. 6: 65-77.

Evenari, M. 1949. Germination inhibitors. Botan. Rev. 15: 153-194.

Fernald, M. L. 1950. Gray's manual of botany, 8th ed. American Book Co., New York.

Funke, G. L. 1941. Essai de phytosociologie experimentale. Bull. Soc. Hist. Nat. Toulouse 76: 19-21.

_____. 1943. The influence of Artemisia absinthium on neighbouring plants. Blumea 5: 281-293.

Garb, S. 1961. Differential growth-inhibitors produced by plants. Botan. Rev. 27: 422-443.

Gray, R., and J. Bonner. 1948. An inhibitor of plant growth from the leaves of Encelia farinosa. Am. J. Botany 35: 52-57.

Hamilton, K. C., and K. P. Buchholtz. 1955. Effect of rhizomes of quackgrass (Agropyron repens) and shading on the seedling development of weedy species. Ecology 36: 304-308.

Hemberg, T. 1947. Studies of auxins and growth-inhibiting substances in the potato tuber and their significance with regard to its rest period. Acta Horti Bergiani. 14: 133.

_____. 1954. Studies on the occurrence of free and bound auxins and of growth-inhibiting substances in the potato tuber. Physiol. Plant. 7: 312-322.

Hitchcock, A. S. 1950. Manual of the grasses of the United States. 2nd ed. revised by Agnes Chase. U. S. Dept. Agr. Misc. Publ. 200.

Hoagland, D. R., and D. I. Arnon. 1938. The water-culture method for growing plants without soil. Calif. Agr. Exptl. Sta. Cir. 347.

Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecol. Monog. 20· 229-250.

Khudairi, A. K., and E. K. Bonde. 1954. Growth inhibitor activity in Xanthium in relation to photoperiodism. Plant Physiol. 29: 533-536.

Konis, E. 1947. On germination inhibitors. VI. The inhibiting action of leaf-saps on germination and growth. Pal. J. Botany, Ser. J. 4: 77-85.

Larsen, P. 1955. Growth substances in higher plants. Moderne Methoden der Pflanzenanalyse. 3: 565-625.

Machlis, L., and J. G. Torrey. 1956. Plants in action. A laboratory manual of plant physiology. W. H. Freeman and Co., San Francisco. pp. 63-65.

Mergen, F. 1959. A toxic principle in the leaves of Ailanthus. Botan. Gaz. 121: 32-36.

Muller, C. H. 1953. The association of desert annuals with shrubs. Am. J. Botany 40: 53-60.

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

Nielsen, K. F., T. F. Cuddy, and W. B. Woods. 1960. The influence of the extract of some crops and soil residues on germination and growth. Can. J. Plant Sci. 40: 188-197.

Ovesnov, A. M., and A. A. Shchekina. 1960. The effect of subterranean parts of couch grass and sow thistle on germination of the seeds of meadow herbs. Doklady 127: 220-222.

Ruge, U. 1939. Zur Physiologie der genuinen Keimungshemmenden und Beschleunigenden Stoffe von Helianthus annuus. Zeits. für Botany 33: 529-571.

Stout, M., and B. Tolman. 1941. Factors affecting the germination of sugar beet and other seeds with special reference to the toxic effects of ammonia. J. Agr. Res. 63: 687-713.

Went, F. W. 1942. The dependence of certain annual plants on shrubs in southern California deserts. Bull. Torrey Botan. Club 69: 100-114.

_____. 1955. The ecology of desert plants. Sci. Am. 192: 68-75.