SMITHSONIAN MISCELLANEOUS COLLECTIONS
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(With Eight Plates)

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CITY OF WASHINGTON
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While attempting to culture oat seedlings in a tightly closed growth chamber constructed from ponderosa pine and hardboard (Masonite Tempered Presdwood),[2] a very marked retardation or arrestment of development was observed. Inasmuch as the plants were not in direct contact with the growth chamber and as normal seedling development was found concurrently in a variety of other containers under identical conditions of temperature, humidity, light, and substrate, the inhibitory effect seemed to be attributable to an emanation from the box. Production or liberation of the active agent was found to continue over a long period of time as inhibition resulted consistently, in undiminished degree, in several trials over a period of some months, despite repeated and prolonged ventilation of the chamber.

This observation seemed to be of sufficient interest to warrant further exploratory experiments on various aspects of the phenomenon.

DESCRIPTION OF PLANT RESPONSE

Air-dry "seeds" planted on a moist germination substrate [3] and placed at once in the box imbibed water readily and development

[1] Now with the Department of the Army, Camp Detrick, Frederick, Md.

[2] The inside dimensions of the box were $91 \times 38 \times 36$ cm., giving a volume of approximately 124,000 cm.^{3}. The area of the inner pine surface was 9,200 cm.^{2}, and of the inner Presdwood surface 6,900 cm.^{2}, or a total of 16,100 cm.^{2}. Prior to use, the interior of the box had been brush-coated with two layers of varnish and allowed to dry thoroughly.

[3] Porous silica wicks (obtainable from Filtros Incorporated, East Rochester, N. Y.) wrapped in filter paper and partially immersed in distilled water contained in finger bowls, as illustrated in plate 1, were used in most of the experiments.

appeared to be initiated normally but, in most plants, ceased completely when the radicles and coleoptiles attained lengths of about a millimeter. Seedlings in this arrested condition could be kept in the chamber as long as 5 weeks without any apparent change. The inhibition was rapidly and completely terminated, however, by transferring the plants to other containers constructed of glass, copper, galvanized iron, or tin plate; after such transfer the seedlings promptly resumed development at a rate at least as great as normal. (See pl. 1.)

Preliminary tests with other species indicated that wheat and corn are affected very much like oats; the germination of sorghum, barley, tomato, bean, lettuce, and radish was also decreased or retarded, but the inhibition was less pronounced than in the foregoing.

In subsequent experiments with oats, described below, it proved possible to achieve a greater degree of inhibition such that even the incipient germination was suppressed. This suggests that the initial development of seeds in the original growth chamber may have been permitted by a lower concentration of inhibitor prevailing at the outset of an experiment, as opening the box necessarily permitted some ventilation.

The susceptibility of the seedlings decreases after the earliest stages of development. Thus, seeds which were allowed to germinate for 2 days in a control chamber and were then transferred to the toxic box exhibited relatively little subsequent retardation, whereas marked inhibition resulted when the foreperiod was 24 hours or less. The result of a similar experiment is shown in plate 2.

Inhibition occurs both in light and in darkness, and on the silica wicks either with or without filter paper. The effect was not found, however, if the seeds were planted on soil or on an agar-water gel (pl. 3).

SOURCE OF THE INHIBITORY EMANATION

The materials of the growth chamber which could be implicated as sources of the emanation were the varnish, the hardboard, and the pine wood.

Varnish.—The particular lot of varnish which had been used in coating the original box was no longer available, but experiments were made with five other brands from different manufacturers; these were tested as dried films on cardboard panels which were enclosed with dishes of seeds in metal containers. All were found to retard seedling development to some extent although in no case was the effect as great as that originally observed. Similar results (pl. 4) were ob-

tained with films prepared from various vegetable oils (linseed, soybean, safflower, and castor) containing lead and cobalt naphthenates as driers. A layer of linoleic acid also was found to cause some retardation of growth; its effectiveness could be increased by exposure, in an open dish, to daylight for several hours prior to the test. Oleic acid, which is less unsaturated than linoleic, had very little inhibitory activity.

These tests indicated that varnishes, vegetable oils, and unsaturated fatty acids give rise to emanations which retard seedling development.[4] However, the effects observed were less marked than those found in the toxic growth chamber, and while the possibility was considered that the difference might be due to more rapid production of the active agent from the original varnish, it seemed desirable to make further tests of the other materials of the box.

Wood.—Accordingly the varnish was removed mechanically from the box with a cabinet scraper; the inhibitory activity was not diminished thereby but rather seemed to be somewhat enhanced. A second box was then built entirely of pine boards (not certainly identified as to species but belonging to the yellow-pine group) which had never been varnished; in this box the inhibition was unmistakably greater than in the first, germination being completely suppressed.

An experiment was next set up in which 10 other species of wood were tested in the form of small pieces of well-seasoned board in desiccators or bell jars. All proved to exert a marked inhibitory action (pl. 5).

All these tests were essentially qualitative, the appearance of the seeds or seedlings being deemed a sufficient criterion of the occurrence of inhibition. It was not thought worth while to attempt to develop a more quantitative measure of inhibition until the factors influencing production and action of the inhibitor were better understood. Furthermore, as the wood samples employed in the previously described experiment were obtained from scraps of lumber of uncertain history, scant significance would appear to attach to the relative effectiveness of the different woods. What relation may exist between the amount of wood present and the magnitude of the inhibition has not been ascertained. Data on weights, volumes, and surfaces of the samples used are presented in table 1.

[4] On the basis of our previous experience with culture of oat seedlings we can conclude that the decrease in oxygen content and increase in carbon dioxide content of the atmosphere (which accompany autoxidation of drying oils and unsaturated fatty acids in closed containers) were much too small, under the existing conditions, to have been of significance as factors in the inhibitory action.

In another experiment, one dish of seeds was placed in a 13-liter desiccator with three pieces of spruce board (total 358 g.) and a second set enclosed in a similar container with an equal weight of small chips (prepared by running a piece of the same board over a planer set at 1/16 inch) which of course possessed a very much greater exposed surface. Both sets were inhibited equally, suggesting that the degree of inhibition is related to weight or volume of wood rather than to surface. No inhibition was found when only one-ninth the weight (40 g.) of chips was present.

TABLE 1.—*Inhibition of oat germination by emanations from various species of wood* (see also pl. 5)

Relative effectiveness	Wood	Weight of wood per cm.^{3} of air in container	Volume of wood per cm.^{3} of air	Surface of wood per cm.^{3} of air
		mg.	cm.^{3}	cm.^{2}
1	Tulip poplar	9	0.020	0.112
2	Spruce	...	...	.110
3	Red oak	126	.166	.336
4	White oak	108	.137	.282
5	Black walnut	50	.091	.228
6	Douglas fir (plyboard)	28	.048	.172
7	Poplar	48	.108	.202
8	Eastern red cedar	165	.293	.634
9	Mahogany	77	.139	.477
10	Black cherry	89	.155	.370

Hardboard.—It remained to test the Masonite Tempered Presdwood [5] such as had been used in construction of the box in which the inhibitory effect was originally observed. This material also was found to produce a toxic emanation.

IDENTITY OF THE INHIBITOR

It is well known that autoxidation of unsaturated fats and of drying oils, such as are used in the formulation of varnish, gives rise to a variety of volatile products (Friend, 1917; Hefter and Schönfeld, 1937; Gardner, 1914a; Vogel, 1930; Lea, 1938). Volatile compounds have been shown also to be present in, or produced by, wood and certain wood constituents (Wise, 1944; Schorger, 1917; King-

[5] According to the manufacturer this material is made from exploded wood fiber, chiefly of southern yellow pine. The lignocellulose fibers are refined, felted, and pressed into board form and then impregnated with a resin compound which is completely polymerized by heating.

zett and Woodcock, 1910, 1912). It has been demonstrated, further, that oxidation of various fats and fatty acids results in development of antibiotic activity [6] (Sabalitschka, 1939; Spoehr et al., 1945, 1946) and that in some instances such activity is due to volatile substances (Harris, Bunker, and Milas, 1932a, b); the reputed sanitary value of oil paints has been ascribed to production of volatile aldehydes (Gardner, 1914b; Hewitt, 1943). The vapors of a number of essential oils, too, have been found to be bactericidal or bacteriostatic (Schöbl and Kusama, 1924; Schöbl, 1925).

On the other hand, some workers have ascribed the antibiotic effects which accompany oxidation of oils to emission of radiant energy (Wrenn, 1927; Ried, 1930).

Radiation versus chemical vapor.—In order to determine whether the growth inhibition of seedlings caused by wood is due to a vapor or to radiant energy emitted by the wood, the following experiments were performed.

In a metal box containing a few small boards were placed two dishes of seeds, one of which was in turn enclosed in a cell with 2.1-mm. thick windows of Corning No. 791 glass. According to the manufacturer, this glass transmits ultraviolet radiation of wave lengths greater than 2200 A. The plants exposed directly to the wood were strongly inhibited while those within the cell, which were protected from any chemical vapor arising from the wood, all developed normally (pl. 6, fig. 1). This experiment demonstrates that no appreciable part of the inhibition by wood can be due to radiation of wave lengths greater than about 2200 A., although it does not eliminate the possibility of activity by shorter wave lengths.

In the second test, dishes of seeds were placed in two similar 1.5-liter bell jars which were connected separately to a compressed-air line. Humidified air was blown through each jar at about 15 liters per hour, the air being directed onto the seeds by means of an inverted glass funnel situated immediately above them. The air supply to one jar was first passed through a metal can containing seven small pieces of board (total weight=770 g.). The plants exposed to air which had been in contact with the wood were markedly inhibited (pl. 6, fig. 2) indicating that the active agent had passed from the wood-containing can to the bell jar. As these were connected by a 40-cm. length of small-bore rubber tubing bent in a semicircle, the conclusion seems inescapable that the inhibitory agent was transmitted as vapor rather than as radiant energy.

[6] Antibiosis is here employed in its broadest sense of an action inimical to normal life processes.

In several experiments in closed vessels containing pieces of wood, a curious effect was noted. In a single population of seeds planted on a silica block of relatively small dimensions, some plants might be inhibited much more than others, but the variation was not distributed randomly through the population as would be expected if it were due to individual differences in susceptibility; rather a positional effect was manifest. That is, plants at one end of the wick might be completely checked while the growth of those at the other end would be only slightly retarded; the seedlings between exhibited an intermediate response. Examples of this behavior are illustrated in plates 2 and 5.

The explanation seems to be that the active vapor is not distributed uniformly in the air of the container. The combined influence of the slow diffusion within a closed vessel maintained at uniform temperature and the relatively rapid removal of the agent from the vapor phase results in concentration gradients within the confined space. To test this hypothesis, two wicks were arranged end to end in a jar and some pieces of board were placed near one end of one of the wicks. A rather striking gradation of inhibition, according to the distance from the wood, resulted (pl. 7, fig. 1). Similar effects are produced also by vapors of known chemicals if the locus of production of the vapor is situated unsymmetrically with respect to the seeds. This was shown unmistakably by seeds exposed to hydrogen peroxide vapor although not so clearly evident in the reproduced photograph (pl. 7, fig. 2); in this experiment, each dish of seeds was in an individual jar with dishes of hydrogen peroxide solution adjacent to the ends of the wicks shown at the right-hand side of the photograph.

Tests on vapor from wood.—Room air was humidified and drawn, by means of a water-line aspirator, through a glass tube (4 m. long, 4 cm. diameter) packed with 350 g. of spruce chips. At a flow rate of approximately 15 l. per hour this air completely checked the development of oat seeds when passed through a desiccator in which they had been planted. A similar set of seeds placed in the air stream ahead of the wood was not inhibited showing that the unaltered room air was nontoxic.

The desiccators were then replaced with gas washing bottles containing 100 ml. of boiled distilled water (pH=7.0) through which the air was passed as fine bubbles during a 5-day period. At the end of this time the water was found to be free of ammonia (<0.01 mg.), hydrogen peroxide (<0.1 mg.), and substances capable of oxidizing potassium iodide in acid solution. The pH of the water in the bottle

following the wood had been lowered to 3.5, however, indicating absorption of an acid substance.

When the air which had passed over the chips was scrubbed through water its inhibitory potency was greatly diminished. Hence the active constituent appears to be absorbed or destroyed by water. Bubbling the air through 5N sulfuric acid did not remove the inhibitor. These results also suggest that the active component may be acidic in nature.

Inhibitory effect of various volatile compounds.—While the above-described experiments were in progress exploratory tests were made with some of the substances which might be expected to be present, in order to determine whether exposure of the seeds to the vapors would result in inhibition similar to that produced by the emanations from oils and wood. Volatile products of autoxidation of unsaturated fats include carbon dioxide, carbon monoxide, organic acids, aldehydes, and peroxides, some of which have been shown to possess a high degree of antibiotic activity.

Carbon monoxide was tested at concentrations of 1, 5, 10, 20, and 25 percent by volume in air. Retardation of germination and of root and shoot growth occurred at concentrations of 10 percent and greater, but even in 25-percent CO the inhibitory effect was much less pronounced than that caused by the emanations from wood.

For the hydrogen peroxide tests (pl. 7, fig. 2) the seeds were placed in 3-liter jars containing open dishes of aqueous H_2O_2 solutions (volume=30 ml.; exposed surface=125 cm.^{2}). It is estimated that air at 25° in equilibrium with 20, 50, and 90 percent solutions, respectively, contains about 0.17, 0.29, and 2.25 mg. H_2O_2 vapor per liter.

Tests of the other compounds were conducted by placing small open vials containing weighed amounts of the liquids, solids, or aqueous solutions (in the case of formaldehyde and acrylic acid) in the desiccators with seeds.

Sufficiently large dosages of several of the compounds were lethal. At lower concentrations development was arrested but could be resumed on subsequent ventilation, thus duplicating the effect of the varnishes, oils, and wood. Continued inhibition without killing appears to require a maintained supply of the vapor but the concentrations necessary for this were not closely determined. It was, of course, possible to calculate the concentrations which would have existed if all the introduced material were present as gas, but as some of the compounds vaporized slowly and as there was, in all likelihood, loss from the vapor phase by absorption, adsorption, or chemical reac-

tion, the actual concentrations were probably considerably lower. The special apparatus and technique required in order to maintain known concentrations in the vapor phase for the 4- or 5-day duration of a test was not warranted in view of the lack of agent-specificity of the inhibition.

Of the compounds tested, the more active were: acrylic aldehyde (acrolein) (see pl. 8), crotonaldehyde, hydrogen peroxide, crotonic acid, and acrylic acid. Also effective, but at higher concentrations, were: acetic acid, propionic acid, n-butyric acid, n-valeric acid, n-butyraldehyde. At the vapor concentrations attainable, little or no inhibition was produced by enanthic acid, caprylic acid, pelargonic acid, capric acid, adipic acid, pimelic acid, or lauroyl peroxide.

Owing to the nonspecificity of the inhibition, the value of these exploratory tests with known compounds is of a negative character in that they serve to eliminate as possibilities those substances found to be relatively inactive but do not differentiate among the more effective ones.

DISCUSSION

The foregoing observations raise numerous questions regarding the nature of the volatile agent (or agents), the mechanism of its formation by diverse materials, the mode of its action on the plant, and its detoxification by some substrates. Further experimentation is required to provide the answers to these.

It cannot be stated whether a variety of antibiotic agents is evolved from varnishes, oils, unsaturated fat acids, and various species of wood, or whether these diverse materials owe their activity to production of a single compound. It seems unlikely that the agent is present as such in these materials; rather it is probably formed through oxidative processes.

From the viewpoint of the inciting materials there is a degree of similarity between the plant inhibition and the so-called "Russell effect" by which is designated the production of a latent image in a photographic emulsion in darkness by a large variety of materials, including woods, resins, terpenes, animal and vegetable oils, and unsaturated fat acids (Russell, 1897, 1898, 1899, 1904, 1906, 1908; Molisch, 1903; Schmidt, 1908; Kugelmass and McQuarrie, 1924, 1925; Baughman and Jamieson, 1925; Haxthausen, 1925; Stutz et al., 1925; Keenan, 1926; Mix, 1944). The agent responsible for this phenomenon can act at a distance, be conducted through a bent tube, and penetrate porous materials such as paper or gelatin but not glass or metals. There is some evidence that the Russell effect is due to production

of hydrogen peroxide vapor, presumably as a result of oxidation of some constituent of the effective materials, although some investigators have attributed it to emission of radiant energy. However, in view of the relatively high concentration of hydrogen peroxide vapor required for inhibition of oats and of the negative test for this compound in the wood aeration experiment, it is improbable that this is the antibiotic agent.

The mechanism of action on the plant is of particular interest in view of the ready reversibility of inhibition. Continuous exposure to the vapor is necessary in order that development remain arrested; there is no evidence of a cumulative effect on prolonged exposure at the concentrations prevailing under the conditions employed. This suggests that there may be a continuous absorption and detoxification of the agent either by the plant or by the external water supply. It is not known whether the vapor is absorbed directly by the seed or must first be dissolved externally.

In contrast to the emanations from wood, the vapors of certain of the toxic chemicals which have been tested are not neutralized by soil or agar (pl. 8). Possibly this difference is merely one of degree and would not be found if the wood vapor could be supplied in greater concentrations.

That an effect so marked as the complete arrestment of development has not frequently been noted by others who have cultured seeds in small unventilated wooden or varnished containers may be due to the detoxifying action of soil, and perhaps also of other organic materials used as substrates. The literature is not devoid of references to more or less similar phenomena. Borriss (1940) presented evidence of the occurrence in air of germination-inhibiting substances whose action was nullified by the use of soil or charcoal as substrate. He believed these vapors to arise, at least in part, from the varnish of his incubators and showed that similar effects were produced by emanations from turpentine, linseed oil, and varnish. Raines (1935) reported that growth of roots was affected by vapors liberated at room temperature from paraffine, "vaseline," mineral oils, and various waxes, and Raines and Travis (1937) attributed seasonal differences in root growth under uniform conditions of light and temperature to ventilation conditions of the laboratory; it was suggested that during the winter months the air contains higher concentrations of vapors from illuminating gas, paints, oils, varnishes, etc. Possibly effects of this kind may have been involved in studies of seasonal variations in seed germination (e.g., Schmidt, 1930; Baldwin, 1935).

Abnormal curvatures, diminished elongation, and increased thickening of seedling shoots cultured in laboratory air have been noted by several investigators (Neljubow, 1901, 1911; Singer, 1903; Richter, 1903, 1906). Similar effects were shown to be produced by low concentrations of ethylene (Neljubow, and also later workers) and of vapors from terpenes and from wood (Richter, 1906).

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SUMMARY

Air in contact with certain oils, varnishes, and woods was found to acquire the property of inhibiting or markedly retarding the germination of oats, wheat, and corn, and also, to less pronounced degree, sorghum, barley, tomato, bean, lettuce, and radish. The inhibition or retardation ceased completely on removal of the seeds from the affected air. As the active agent could be transferred in an air stream from one container to another, it is considered to be of the nature of a chemical vapor rather than some form of radiant energy.

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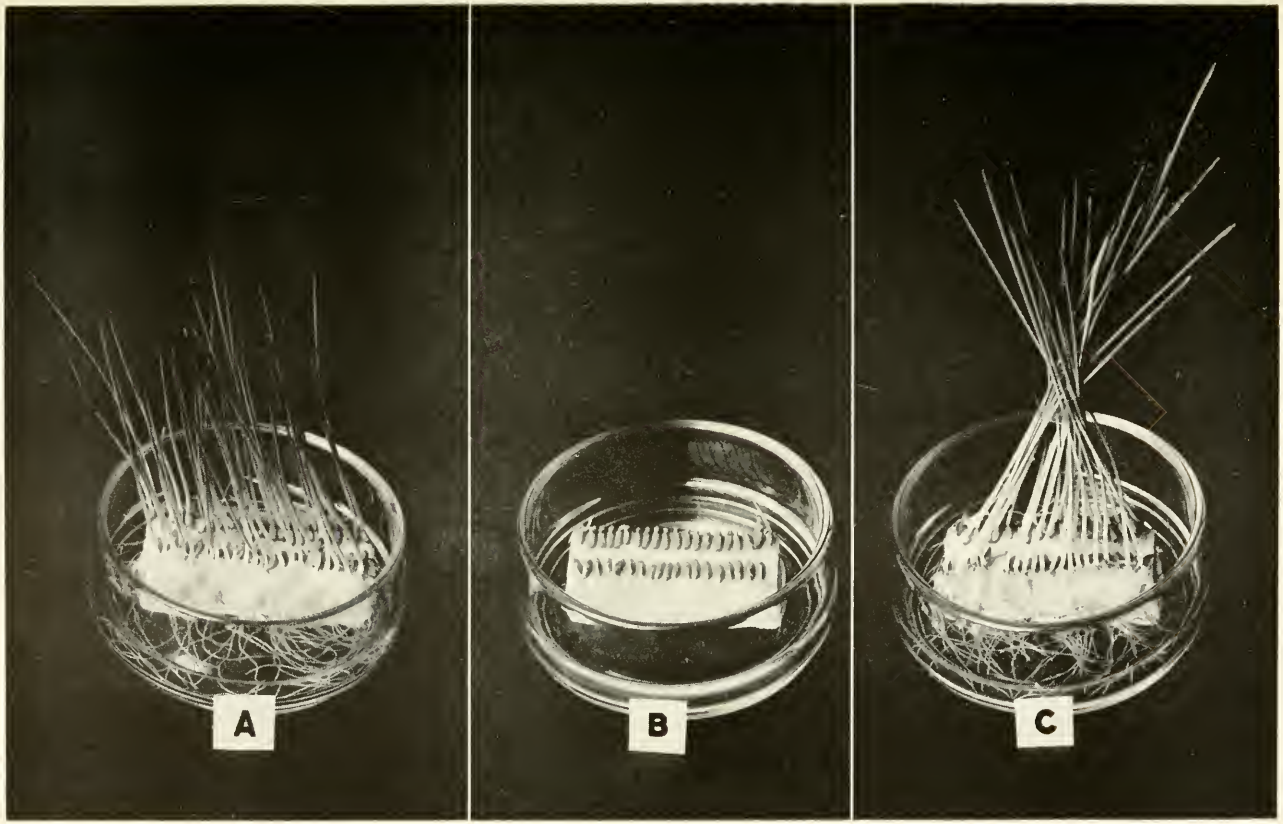
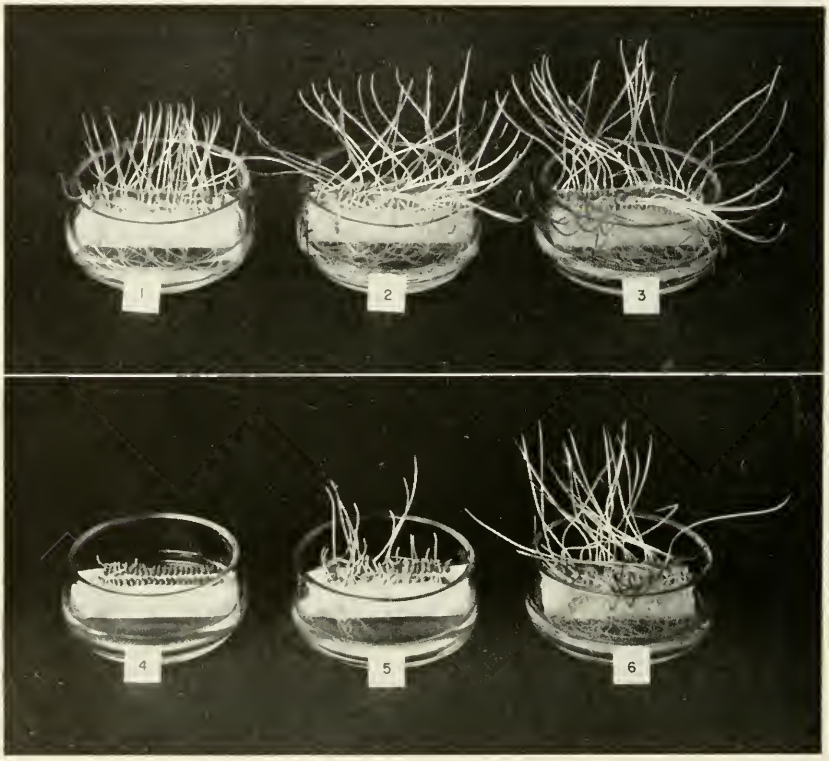


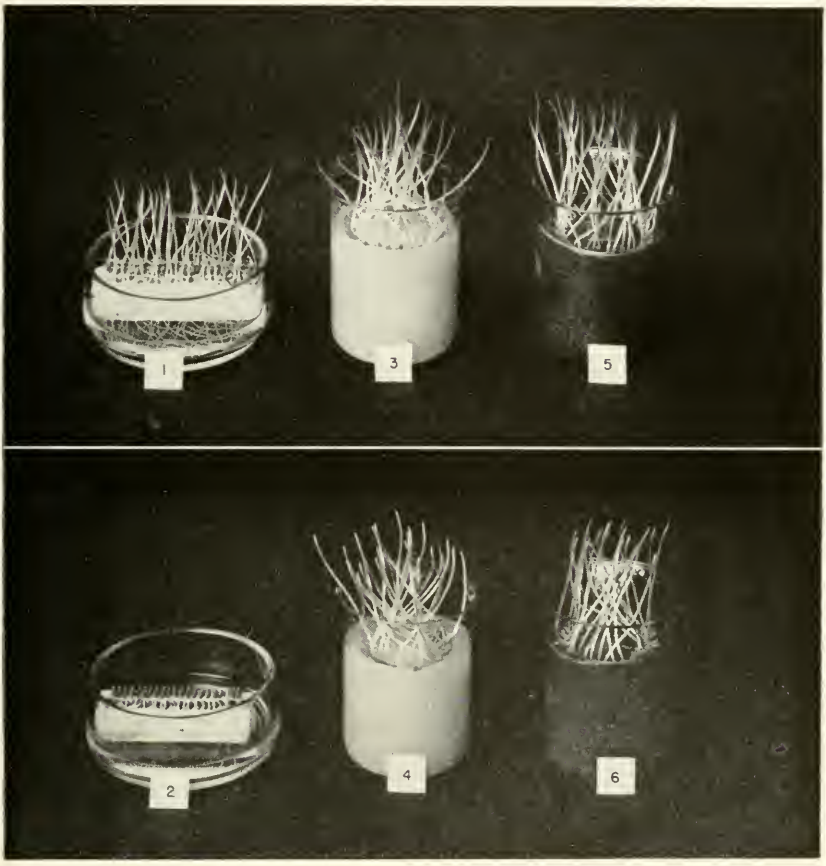
INHIBITION OF OATS BY EMANATION FROM VARNISHED BOX

A, control plants, 5 days after planting; B, planted at same time as set A and kept in varnished box 5 days; C, same plants as in B after having been transferred to control chamber for 5 days.



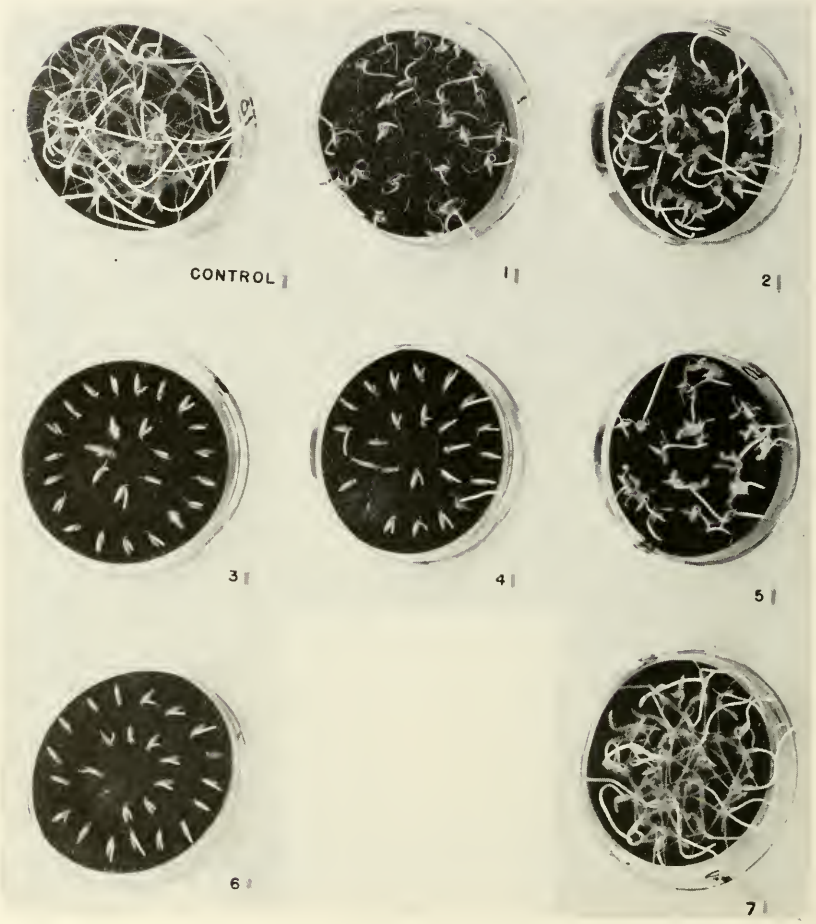
SUSCEPTIBILITY OF OAT SEEDLINGS TO EMANATION FROM WOOD AS INFLUENCED BY AGE AT EXPOSURE

1, 2, 3, controls, aged 5, 6, and 7 days, respectively; 4, age 5 days, exposed to wood from time of planting; 5, age 6 days, exposed to wood after first 24 hours; 6, age 7 days, exposed to wood after first 48 hours.



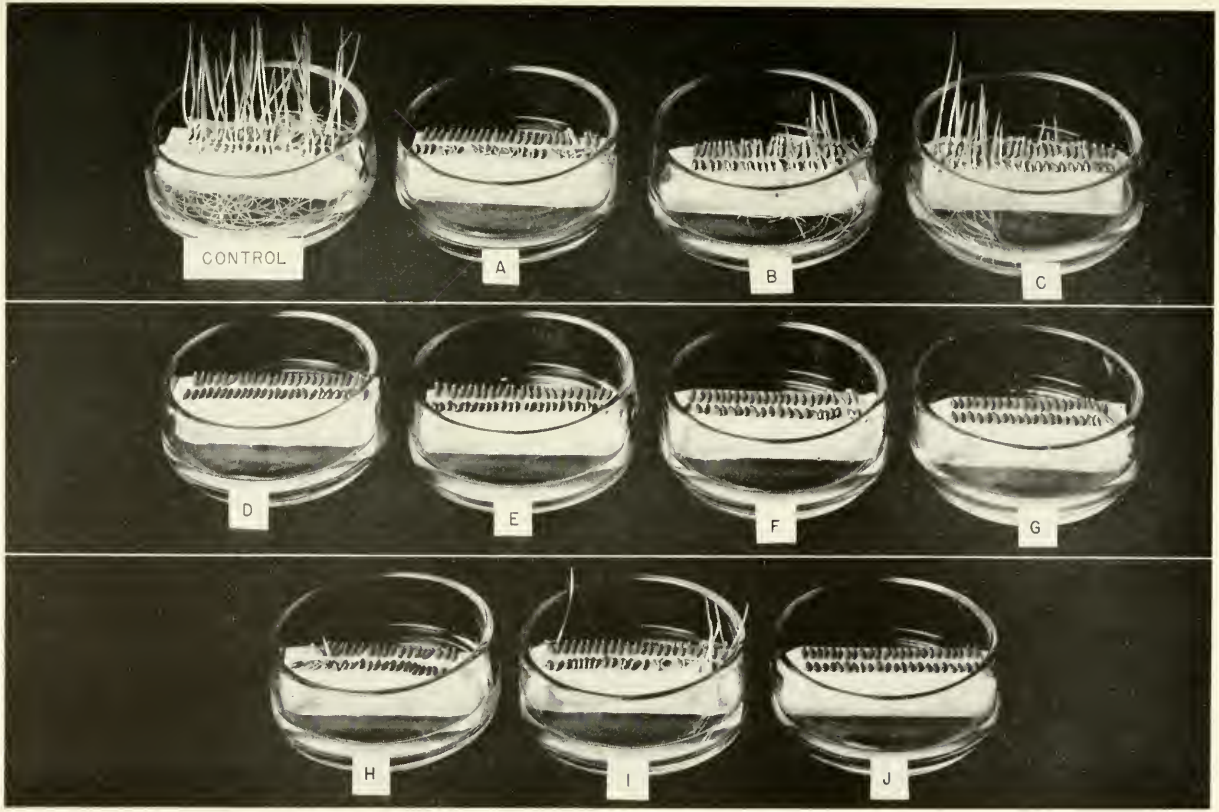
INFLUENCE OF SEED SUBSTRATE ON INHIBITION BY EMANATION FROM WOOD

1, 3, 5, controls, in 18-liter galvanized iron box; 2, 4, 6, cultured in similar box containing 7 pieces of wood (total weight = 780 g.). 1, 2, seeds planted on filter-paper-wrapped silica wicks; 3, 4, seeds planted on 1.5-percent agar gel; 5, 6, seeds planted on garden loam. Photographed 4 days after planting.



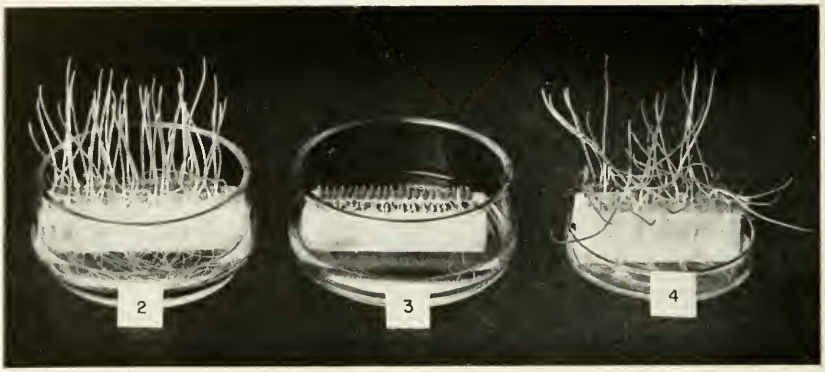
INHIBITION BY EMANATIONS FROM VEGETABLE OILS

Oat seeds planted on blotters in open dishes were cultured in closed 1-liter cans containing cardboard panels coated with various oils: 1, "Kellin"; 2, "Kellsoy"; 3, safflower oil; 4, soybean oil; 5, "Dorscolene"; 6, linseed oil; 7, castor oil. Photographed 4 days after planting.



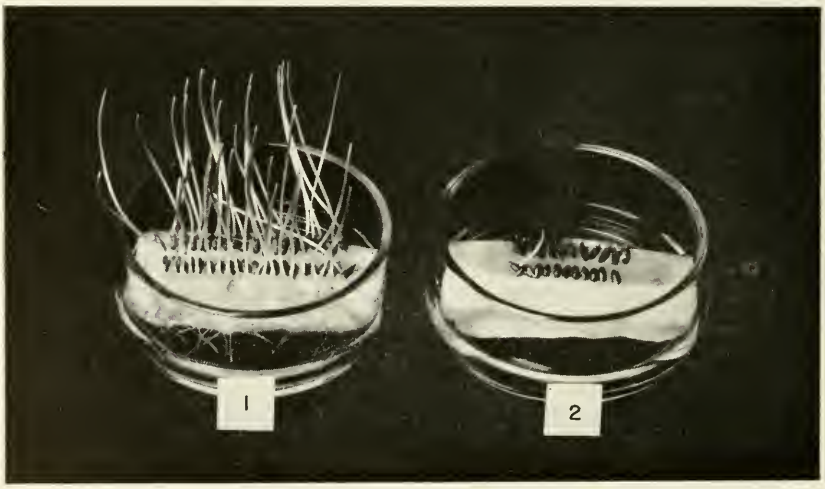
INHIBITION BY EMANATION FROM VARIOUS SPECIES OF WOOD

A, eastern red cedar; B, mahogany; C, black cherry; D, red oak; E, walnut; F, white oak; G, spruce; H, Douglas fir (plyboard); I, poplar; J, tulip poplar.



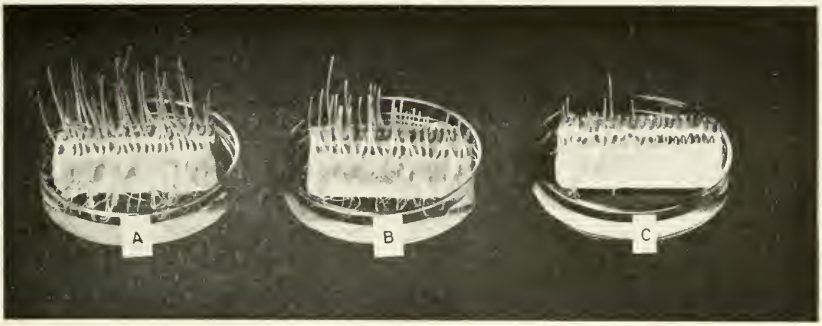
1. OPACITY OF ULTRAVIOLET-TRANSMITTING GLASS TO INHIBITORY ENAMATION FROM WOOD

2, control; 3, 4, cultured in a single closed metal box containing wood. No. 3 was exposed directly to the wood, while No. 4 was further enclosed in a cell with windows of Corning # 791 glass which transmits > 2200 A. (The prostrate position of some of the shoots in No. 4 is due to their having been dislocated on removal from the cell.) Photographed 4 days after planting.



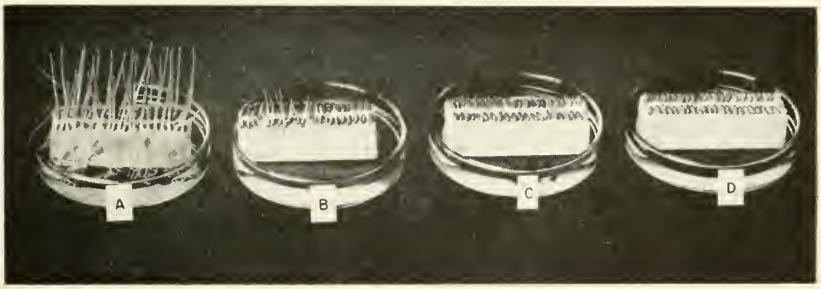
2. INHIBITION BY VAPOR FROM WOOD

1, control, aerated directly from compressed-air line; 2, exposed to air stream which was first passed through can containing wood. Photographed 4 days after planting.



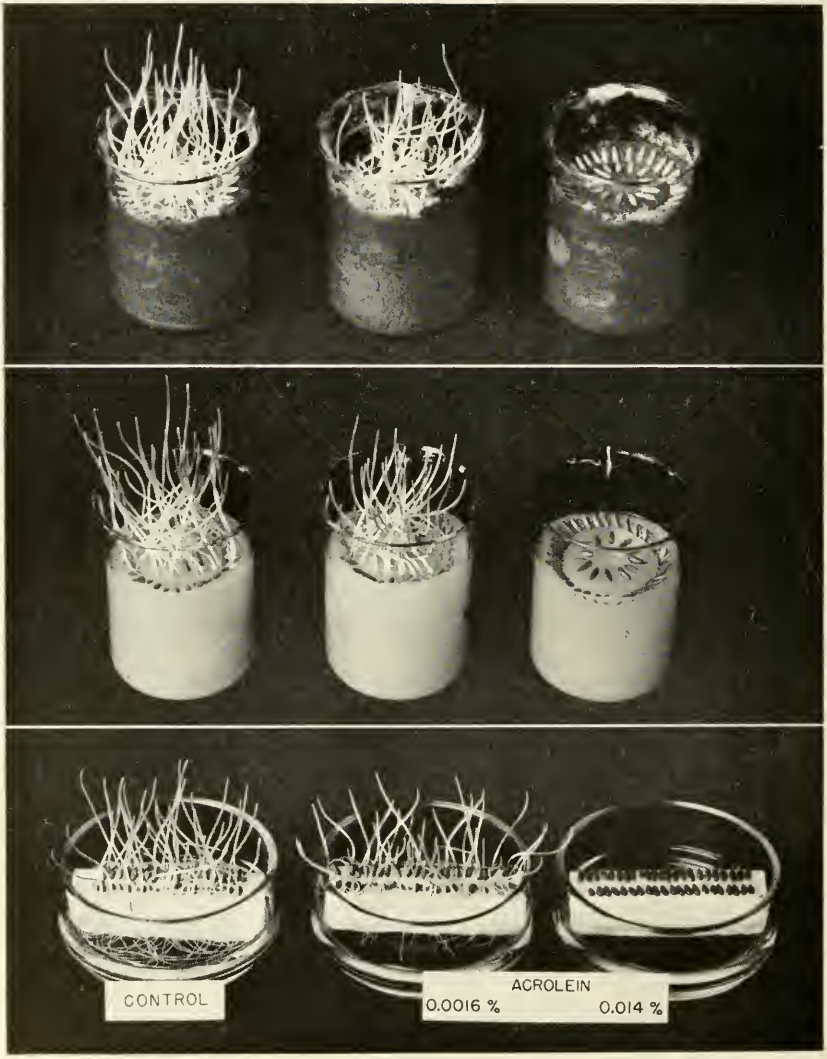
1. INHIBITORY EFFECT OF WOOD AS INFLUENCED BY DISTANCE FROM SEED

A, control; B, C, cultured in single jar in presence of wood. Seeds at right-hand end of C were closest, and those at left-hand end of B were farthest from the wood. Photographed 4 days after planting.



2. INHIBITION BY HYDROGEN PEROXIDE VAPOR

A, control; B, cultured in jar containing dish of 20-percent H_2O_2 solution; C, cultured in jar containing dish of 50-percent H_2O_2 solution; D, cultured in jar containing dish of 90-percent H_2O_2 solution. Note greater inhibition and bleaching of seeds at right-hand ends of wicks, which were closest to H_2O_2 solutions. Photographed 4 days after planting.



INHIBITION BY VAPOR OF ACROLEIN

Seeds planted on garden loam (upper row), 1.5-percent agar-water gel (middle row), and filter-paper-wrapped porous silica wicks (lower row). At the higher concentration (0.014 percent by volume of air) the seeds were killed and did not recover on subsequent exposure to pure air. Photographed 4 days after planting.