THE EFFECT OF THIOUREA WITH AND WITHOUT HEAT ON THE BREAKING OF DORMANCY AND PRODUCTION OF SECONDARY DORMANCY IN DOUGLAS FIR SEEDS

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TABLE OF CONTENTS

THE EFFECT OF THIOUREA WITH AND WITHOUT HEAT ON THE BREAKING OF DORMANCY AND PRODUCTION OF SECONDARY DORMANCY IN DOUGLAS FIR SEEDS

INTRODUCTION

The delay in germination which normally is observed in seeds of various temperate-zone plants, especially trees and shrubs, is evidence of some type of dormancy. It can often be eliminated by means of pre-treatment of the seed in a moist medium at low temperature, a process known as stratification. This is in imitation of the process occurring in nature. The length of time for the stratification depends on the kind of seeds; conifer seed dormancy may be overcome by moistening with water and storing for seven to 14 days at 5° C. (31) (32).

Very little success has attended efforts to break dormancy by chemical means. Deauber (15) was able to shorten the rest period of red and black oak acorns by immersion in a solution of thiourea or by vapors of ethylene chlorohydrin. Johnson (22) has been able to substitute chemical treatments for stratification in the germination of some forest tree seeds. These treatments included soaking in one to four per cent potassium nitrate solution, 1.5 to six per cent thiourea, 1.5 to six per cent ethylene glycol, and dusting with red copper oxide and zinc oxide. Significant increases in germination of

red pine and white spruce with two per cent potassium nitrate over stratification were obtained. Thiourea has been successful in forcing the germination of freshly harvested lettuce seeds at temperatures that ordinarily inhibit germination (36).

Certain environmental conditions such as high temperature may so alter the behavior of stratified seeds that they will not germinate when shifted to a favorable environment for growth. Dormancy induced in seeds by unfavorable germination conditions has been called "secondary dormancy" (12).

This paper presents an investigation of the effect of thiourea on the germination of Douglas fir seeds with and without heat treatment. The effect of these treatments on secondary dormancy was an important objective.

LITERATURE REVIEW

Dormancy

Dormancy in seeds has long been studied. The early literature has been adequately reviewed by Cram (10), Crocker (11), Barton (5), Barton and Crocker (6), Crocker and Barton (12), Miller (28), and Balwin (3). Seeds that fail to germinate even when they are ripe and placed under conditions favorable to germination are assumed to be dormant. This may be the result of structure or the innate physiology of the embryo. Meyer (27) restricted the term "dormancy" to seeds which fail to germinate as a result of internal causes. For convenience, the term "quiescence" designates the failure of a plant organ to grow when this is the result of environmental conditions. Without an experimental test, it is often difficult to determine whether seeds or other plant organs under natural conditions are actually dormant or merely quiescent.

Germination

Factors which give rise to dormancy of seeds may be due to the seed coat, to a physiological state of the embryo, or to some chemical inhibitor. The seed coat or mechanical factor may be due to structural characteristics

which cause impermeability to water or probably to oxygen. The physiological condition of the embryo requires that it undergo certain changes before germination can occur. These may require specific conditions. Chemical inhibitors may need to be leached from the seed coat or otherwise removed.

Most of forest tree seed dormancy appears to be related to the physiological condition of the embryo (18) (28) (30). Germination of Douglas fir seed seems to be little or not at all affected by the seed coat, which is relatively thin and apparently does not interfere with germination.

Breaking Dormancy

Mirov (29) indicated that forest tree seeds sown in a germinator without preceding treatment often fail to germinate. This is true in the case of coniferous trees. Under natural forest conditions in temperate climates between the time of shedding seed in the fall and germination the following spring is a more or less prolonged period of low temperature with abundant moisture. Accordingly, in the artificial germination of coniferous seeds, and this is also true for many broad-leaf species, this natural pregerminative chilling or stratification is often

desirable and sometimes indispensable. If germination of seed is not prompt, but rather scattered over a long period of time, it is frequently an indication that the seed needs stratification. Consequently, it has become usual to stratify all coniferous seeds before planting. There are 13 native species of pine which do not require stratification listed in the "Woody Plant Seed Manual" (39). Even so, many investigators (4) (29) (41) have pointed out that when some of these species are stratified they germinate more quickly and at a more uniform rate than when they are not stratified. Stone (34) proposed that a difference in degree rather than a difference in kind is indicated in these groups. The same metabolic pattern might well prevail in both groups of conifers while the level of substrate, auxin, co-factors, and inhibitors might be different. However, stratification is sufficient to overcome dormancy in these seeds.

Chemicals have been employed in breaking dormancy by many investigators (5) (8) (15) (22). Chemical treatment was tested in comparison with stratification by Johnson (22) on the seeds of a number of species of forest trees. Chemical treatment may replace stratification. Among the agents which significantly increased germination of Larix decidua, Picea abies, etc. was thiourea.

Thiourea is known to be active in many biological processes. In animal organs it affects metabolism, alters mitosis, and inhibits various oxidative enzyme systems (16) (17) (23) (33). Thiourea also has been known as an anti-oxidant used in industry. In plants it is best known for its effects in breaking dormancy and stimulating germination (15) (26) (38). Lettuce seeds treated with thiourea germinate at high temperatures (25° to 35° C.), and the germination rate was greatly increased (36).

Secondary Dormancy

Secondary dormancy is defined by Thornton (37) as the induced dormancy which is a contributing factor in increasing the life span of seeds in nature. Both seeds having primary dormancy and those normally showing no dormancy in the embryo may frequently be made dormant by exposure to adverse conditions if they are held fully imbibed on moist substrate or buried in the soil. Usually the promoting factors are temperature and gas exchange, which are believed to be interrelated. Lack of sufficient oxygen to the embryo may alter the metabolism and cause specific chemical changes which prevent normal functioning. Weiss (42) indicated that the cause of secondary dormancy appears to be due to restricted respiration at high temperatures.

Davis (14) reported that dormancy may be induced in the after-ripened embryos of ragweed, Ambrosia trifida L., by means of high-temperature germination along with restricted oxygen supply caused by impermeability of the seed coats to oxygen. Many studies have shown that seeds vary widely in oxygen requirement (2) (24) (25) (35). The amount of oxygen necessary for germination might be related either to the efficiency of an aerobic respiratory system or to the degree of tolerance to accumulation of toxic anaerobic respiratory products. Bortwick and Robins (7) reported that the oxygen requirement of lettuce seeds increases rapidly with temperature. At low temperatures the oxygen is less restricting.

After maturity a seed may undergo largely unknown processes known as "after-ripening" which are necessary before the seed will grow. After-ripened seed commonly has a lower minimum temperature for germination (7) (9) (14) (19) (40).

Allen reported in 1941 (1) on light and temperature as factors in germination of the seeds of Douglas fir. The germination temperature within the range studied (21° to 35° C.) has no effect upon the rate of germination or upon the total germination of stratified seeds. On the other hand, the untreated Douglas fir seeds at maximum

temperature require a longer time to reach the same total germination as stratified seed. Grose (21), in a study of eucalyptus seeds, obtained evidence that stratification at 40° F. promoted germination of some dormant seeds and increased the germination rate of seeds that exhibited delayed germination. The primary dormancy of some eucalyptus seed is increased by moist storage at temperatures of 63° F. or greater. Temperature conditions unfavorable for germination of stratified seeds often induce a secondary dormancy. Griesbach and Paul (20) working with dormancy and germination of Hemerocallis seeds, present the view that the seeds which do not exhibit deep-seated embryo dormancy usually show a percentage of germination without pretreatment of any sort. The variation of germination rate existing within a seed population at a particular time is undoubtedly due to inherent morphological and physiological differences of individual seeds. Basically the same pattern of germination was observed for non-after-ripened seed. These also show an increased temperature range for germination following cold treatment. Results obtained with excised embryos indicate that this is essentially due to after-ripening. Stratification appears to result in a diminution of the inhibitory action of the enveloping structures of the embryo except at

relatively high temperature. Two of several hypotheses are that after-ripening either decreases the oxygen requirement for germination or alters the structure of the enveloping tissues resulting in increased permeability to oxygen. In the first hypothesis, the reduced oxygen requirement might be the result either of increased efficiency of the energy releasing mechanism or reduced competition for oxygen following saturation of other oxygen-requiring processes.

MATERIALS AND METHODS

Samples of 100 Douglas fir seeds were selected from a hand-harvested lot of seed made by Denis Lavender. Only apparently sound seeds were selected for the sample. Although the sample of seeds had been processed by hand, there was some dormancy of the seed lot. To remove any traces of dormancy, the seed was stratified by placing the sample on moist paper towels and maintaining it at a temperature of 5° C. for three weeks. This treatment is generally accepted as adequate to permit rapid germination.

One per cent aqueous thiourea solution was used in all of the thiourea treatments. Heat was provided by a constant-temperature oven. Treatments with thiourea alone consisted of merely soaking the dry seeds in 1 per cent thiourea for 24 hours at room temperature, then removal from the thiourea and germination on paper towels wet with distilled water. Stratified seeds were taken directly from the 5° C. incubator and treated immediately. Control samples with and without thiourea were germinated at room temperature. Previous experiments had indicated that room temperature was adequate to insure good germination.

The following treatments of 100-seed samples were run in duplicate:

1. Stratified seed was exposed to a temperature of 36° C. for 24 hours then germinated at room temperature for 42 days.

2. Stratified seed was treated with 1 per cent thiourea at 36° C. for 24 hours then germinated for 42 days.

3. Stratified seed was treated with 1 per cent thiourea at 36° C. for 24 hours, then with 1 per cent thiourea at room temperature for 24 hours, then germinated for 42 days.

At the end of the treatment period with thiourea, the seeds were transferred to germinate in petri dishes wetted with distilled water.

The same series of treatments were carried out at temperatures of 38° C., 40° C., and 42° C. A similar set of experiments was performed with seed which had not been stratified. This seed had been hand-harvested and had not been exposed to any heat drying and had been stored in a refrigerator since harvest. It was not especially dormant.

The germination tests were done at room temperature after the various treatment conditions as listed above. The seeds were placed on paper toweling in petri dishes and wet with distilled water. The seeds were kept moist throughout the period of germination. Each petri dish contained 100 seeds.

Germination was indicated by emergence of the primary root. The counts were made when the radicles were about one centimeter in length. Germinated seeds were removed at each count. The number of germinated seeds at each count was noted and recorded as the percentage of germination in the sample. The average of two samples is recorded in the results. In order to differentiate the effect of the factors involved in germination, rate of germination per day was calculated for each interval. The curves are plotted as total percentage and rate of germinations.

RESULTS

Dry seeds of Douglas fir were soaked with thiourea for 24 hours, removed from thiourea and germinated at room temperature for six weeks. While the final germination percentages were similar (Figure 1), the rate of germination, as shown by peaks of the curves in Figure 2, demonstrated that germination was hastened slightly by thiourea treatments.

The stratified seeds germinated much more rapidly in all treatments with and without thiourea. The rate of germination is shown by peaks in Figure 2. Water alone shows a higher germination rate than thiourea at all temperatures. However, the final germination rate is very nearly the same for all samples.

At 36° C. the total percentage of germination of non-stratified seeds, as shown in Figure 3, is 41.5 per cent, which is lower than the total percentage of germination at room temperature, 53.5 per cent. This is probably a temperature-induced secondary dormancy. When thiourea is added to the 36° treatment, the percentage of germination is 14.5 per cent, the lowest percentage of germination in the 36° C. series. If the preceding treatment is followed by treatment at room temperature for 24 hours, the germination is 29.5 per cent, indicating that dormancy may have

The Germination Rate at Room Temperature of Douglas Fir Seeds With and Without Treatment With 1 per cent Thiourea. Series of Treatments Without Heat.

Figure 1. Total percentage of germination without heat treatments of stratified and non-stratified seeds.

Figure 2. Germination rate without heat treatments of stratified and non-stratified seeds.

Curve 1. Non-stratified seeds soaked in 1 per cent thiourea for 24 hours at room temperature.

Curve 2. Non-stratified seeds soaked with distilled water.

Curve 3. Stratified seeds soaked with distilled water (5° C. and R. T. dist. water).

Curve 4. Stratified seeds soaked with 1 per cent thiourea for 24 hours at room temperature (5° C. and R. T. thio.).

(21-day period of stratification for curves 3 and 4 is indicated by "a" on the figures.)

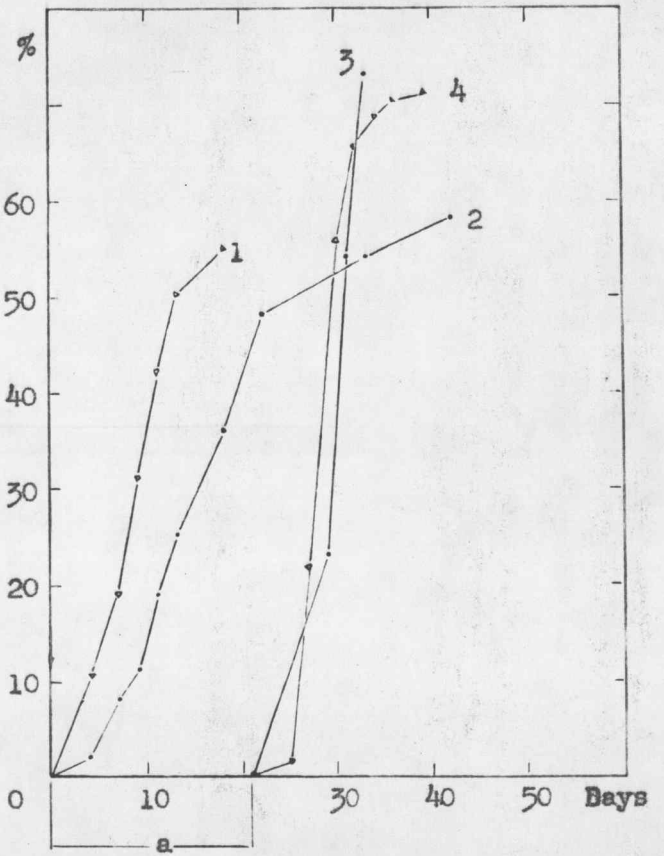

Figure 1.

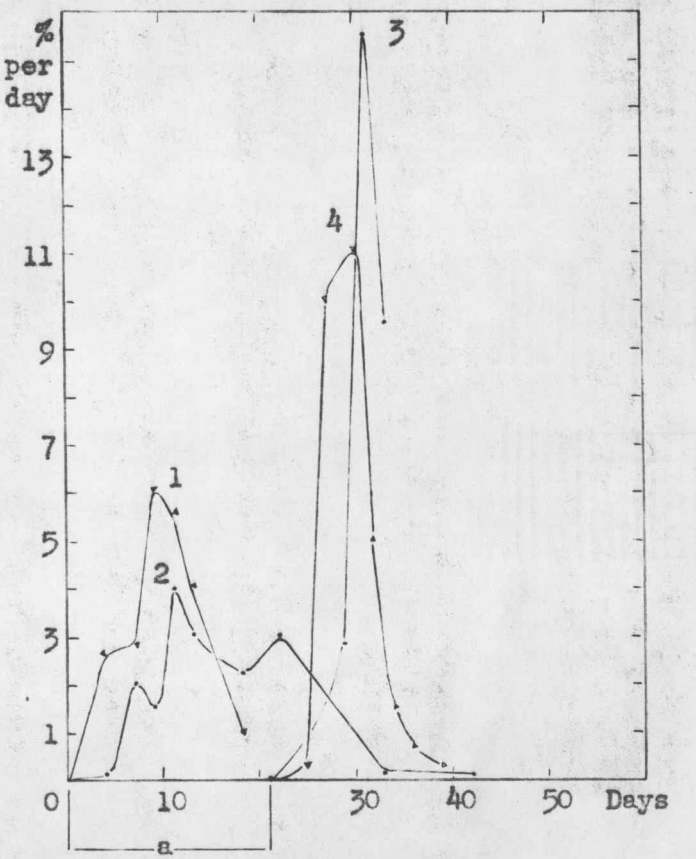

Figure 2.

The Germination Rate at Room Temperature of Douglas Fir Seeds Treated with Water and 1 per cent Thiourea Solution at 36° C. for 24 Hours.

Figure 3. Total percentage of germination of stratified and non-stratified seeds.

Figure 4. Germination rate of stratified and non-stratified seeds.

a. Period of stratification 21 days.

Curve 1. Non-stratified seeds treated at 36° C. in water.

Curve 2. Non-stratified seeds treated at 36° C. with 1 per cent thiourea for 24 hours.

Curve 3. Non-stratified seeds treated at 36° C. with 1 per cent thiourea for 24 hours and then at room temperature with 1 per cent thiourea for 24 hours.

Curve 4. Stratified seeds treated the same as in number 1.

Curve 5. Stratified seeds treated the same as in number 2.

Curve 6. Stratified seeds treated the same as in number 3.

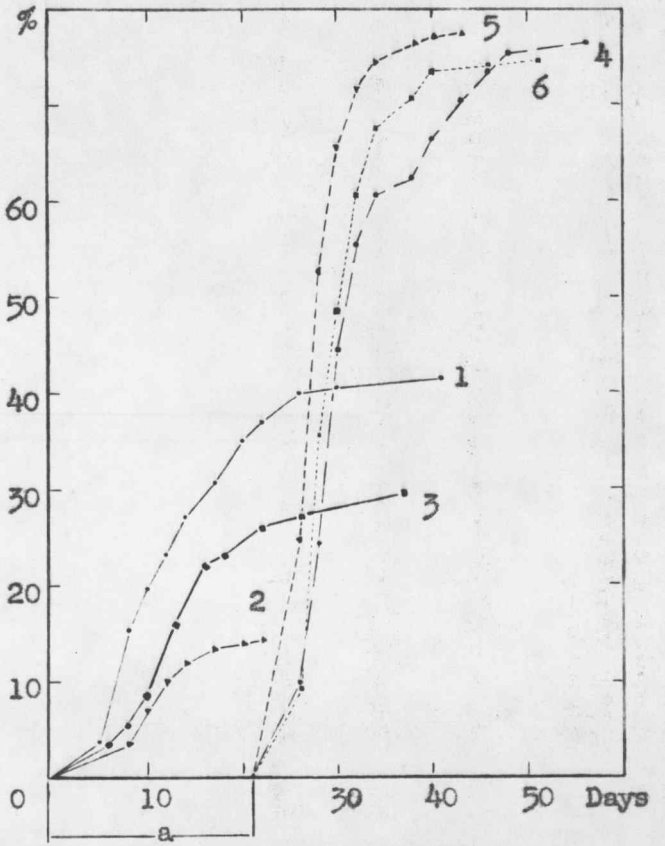

Figure 3.

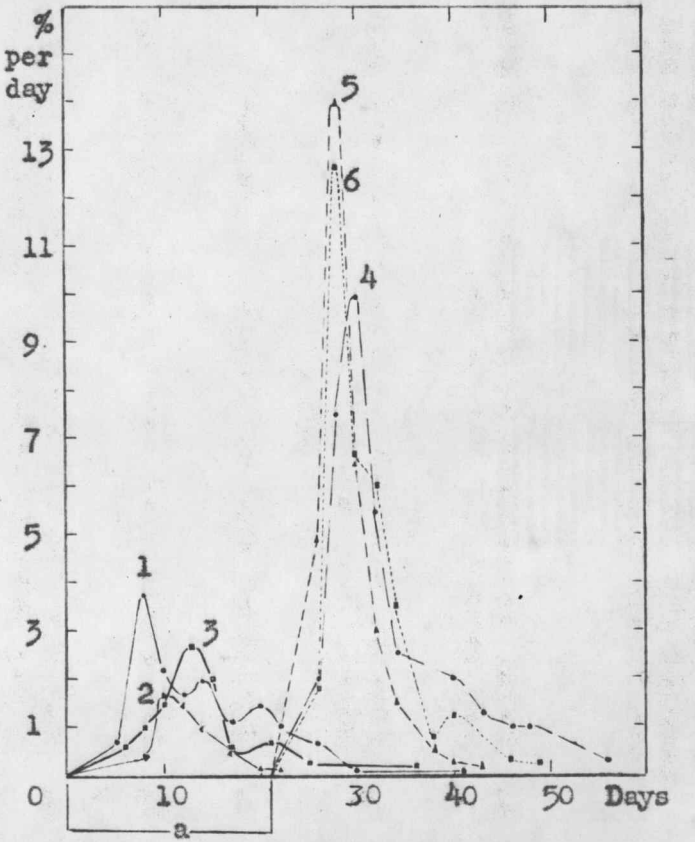

Figure 4.

been broken again. Although at room temperature thiourea hastens germination presumably by breaking dormancy, at higher temperatures it appears to induce a secondary dormancy or at least it accelerates the induction of a secondary dormancy. In stratified seeds treated for 24 hours at 36°, thiourea appears to show an accelerating effect on germination (Figure 4), but the difference may not be significant. However, the real effect of the thiourea on the non-stratified seeds is interesting in contrast to this apparent lack of effect on stratified seeds.

At 38° C. the effect of thiourea on inducing dormancy is even more marked (Figures 5 and 6). Treatment of the seeds for 24 hours at 38° reduces germination of untreated seeds from about 43 per cent to 28 per cent and of stratified seeds from 77 per cent to 58 per cent. However, thiourea reduces the germination of both lots by approximately half when compared to controls. While the treatment with thiourea at room temperature for an additional 24 hours has little effect on the unstratified seeds, whether this is toxicity or dormancy can not be ascertained from these data.

At 40° C. the effect of both temperature and thiourea is considerable. Temperature alone inhibits germination, but thiourea in addition to heat stops germination almost

The Germination Rate at Room Temperature of Douglas Fir Seeds Treated with Water and 1 per cent Thiourea Solution at 38° C.

Figure 5. Total percentage of germination of stratified and non-stratified seeds.

Figure 6. Germination rate of stratified and non-stratified seeds.

a. Period of stratification 23 days

Curve 1. Non-stratified seeds treated at 38° C. with water.

Curve 2. Non-stratified seeds treated at 38° C. with 1 per cent thiourea for 24 hours.

Curve 3. Non-stratified seeds treated at 38° C. with 1 per cent thiourea for 24 hours and then treated at room temperature with 1 per cent thiourea for 24 hours.

Curve 4. Stratified seeds treated as in number 1.

Curve 5. Stratified seeds treated as in number 2.

Curve 6. Stratified seeds treated as in number 3.

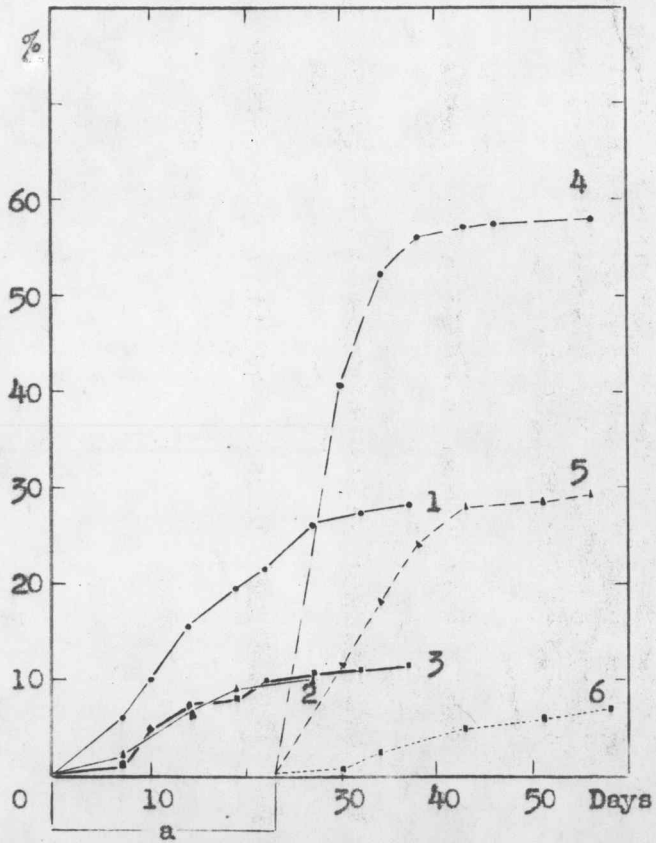

Figure 5.

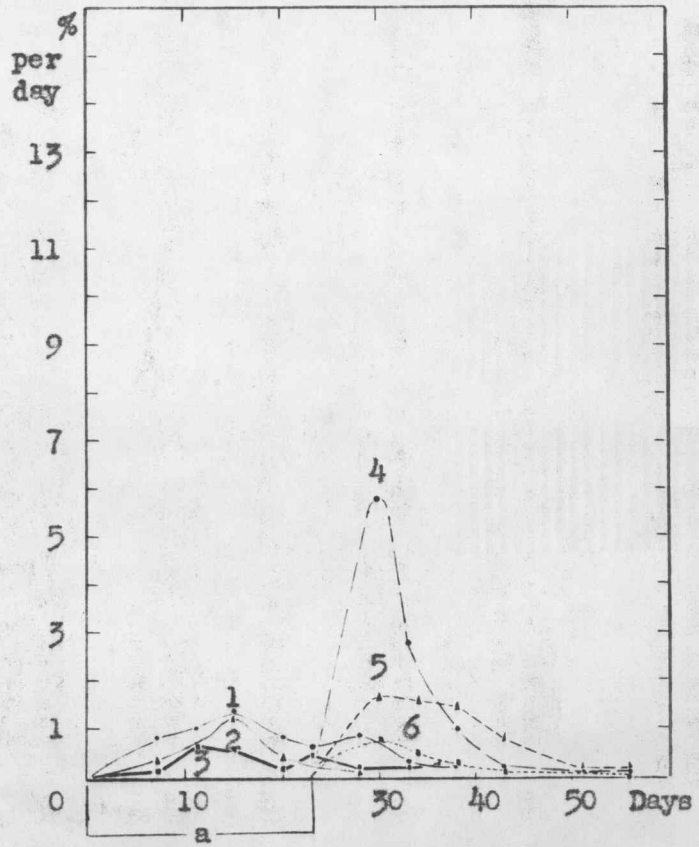

Figure 6.

completely. It is interesting that at this temperature thiourea following heat treatment appears to have a favorable effect on germination.

Treatment at 42° C. is sufficient to cause complete loss of germination both with and without thiourea. Preliminary studies not reported here have shown that this is dormancy rather than death of the seed. Again at 44° C. there was complete loss of germination.

The Germination Rate at Room Temperature of Douglas Fir Seeds Treated with Water and 1 per cent Thiourea Solution at 40° C.

Figure 7. Total percentage of germination of stratified and non-stratified seeds treated at 4o° C.

Figure 8. Germination rate of stratified and non-stratified seeds treated at 40° C.

Figure 9. Total percentage of germination of stratified and non-stratified seeds treated at 42° C.

Figure 10. Germination rate of stratified and non-stratified seeds treated at 42° C.

a. Period of stratification 21 days.

Curve 1. Non-stratified seeds treated at 40° C. with water for 24 hours.

Curve 2. Non-stratified seeds treated at 40° C. with 1 per cent thiourea for 24 hours.

Curve 3. Non-stratified seeds treated at 40° C. with 1 per cent thiourea for 24 hours and then treated at room temperature with 1 per cent thiourea for 24 hours.

Curve 4. Stratified seeds treated as in number 1.

Curve 5. Stratified seeds treated as in number 2.

Curve 6. Stratified seeds treated as in number 3.

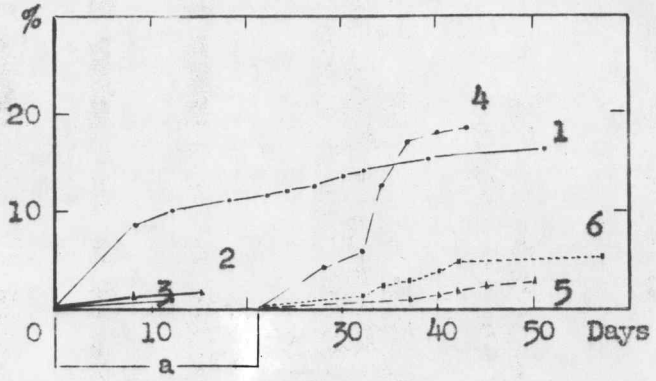

Figure 7.

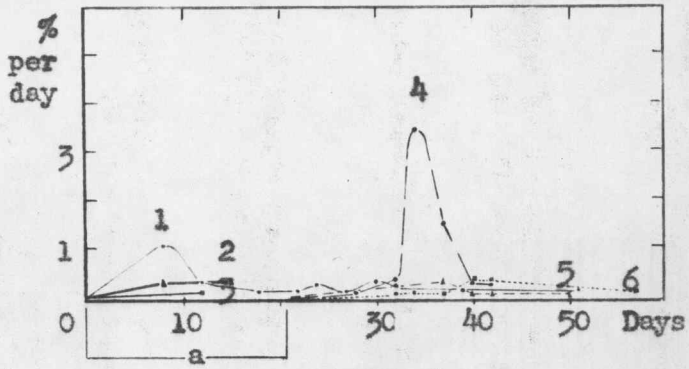

Figure 8.

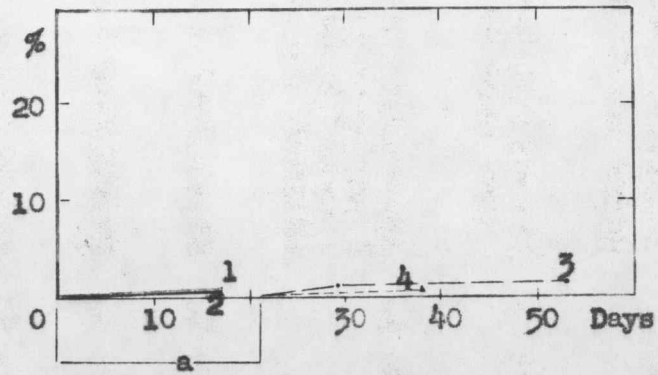

Figure 9.

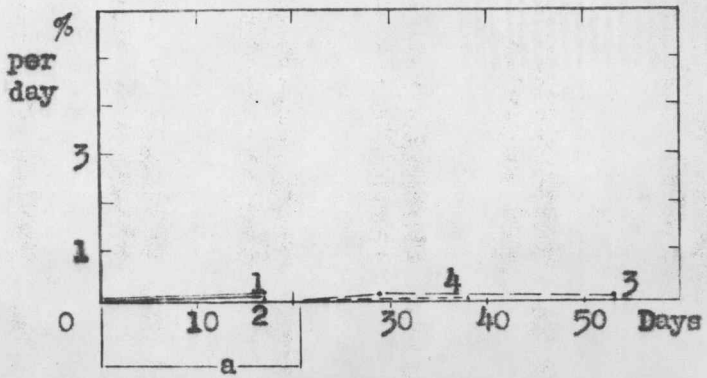

Figure 10.

DISCUSSION

This seed was hand-harvested and cleaned with special precautions to prevent exposure to heat. Consequently, it was only partially dormant as it came from the refrigerator. This was done deliberately in order to make secondary dormancy as obvious as possible.

Treatment with thiourea produced only a small effect on total germination of non-stratified seeds. However, germination was somewhat more rapid at room temperature. With this lot of seed, thiourea would have had little beneficial effect in the field unless prompt germination were especially desired.

Stratification produced better total germination and a more uniform and prompt germination. As would be expected, thiourea did not stimulate stratified seeds. Stratification overcomes dormancy and permits germination to occur rapidly over a wide range of temperatures. Since the known effects of thiourea are limited to breaking dormancy, no effect would be expected.

The effect of stratification on increasing total germination has puzzled seed analysts for many years. Perhaps the best explanation for this phenomenon is that stratification permits more rapid germination and thus a seed lacking in vigor would germinate before it was killed

by some factor in the environment, physical or biotic.

Heat or high temperature induces secondary dormancy with non-stratified seeds at 36° C. However, with stratified seeds this first becomes important at 38° C. Between 38° and 40° C. this effect becomes pronounced with all samples, and at 42° inhibition is complete. These data would indicate that loss of germination will occur at a lower temperature with partially dormant seeds than with non-dormant or stratified seeds.

Thiourea with heat causes marked decrease in the percentage of germination, presumably by promoting secondary dormancy. Secondary dormancy for the non-stratified seeds first appeared at 36° C., presumably because these seeds were more nearly dormant. With increasing temperature, especially in the presence of thiourea, secondary dormancy became more pronounced. When seeds were treated an additional 24 hours at room temperature with thiourea, it appeared to have little influence in breaking secondary dormancy.

The effect of thiourea in increasing the effect of heat in producing secondary dormancy is unexpected, since it has not been reported previously.

The only reasonable explanation that can be offered to explain this effect is that the sulfhydryl group of the

thiourea acts as a catalyst for the specific reaction or reactions involved in production or loss of dormancy. In a way this is a reasonable explanation, since dormancy is a plant response and probably involves an enzymatic mechanism. Temperature may be the controlling factor, with thiourea acting only to accelerate the reaction.

Additional studies with other sulfhydryl reagents such as cysteine, glutathione, mercaptoacetic acid, etc. will probably throw additional light on this question. However, some of these reagents are very difficult to use, since they oxidize in the presence of atmospheric oxygen which is, of course, a requirement for germination.

SUMMARY

For a particular lot of hand-harvested seed, thiourea had a small effect in accelerating germination but no effect on total germination. Heat produces a marked secondary dormancy which is more marked in the presence of thiourea. At 36° C. only non-stratified seeds showed a marked response to thiourea. At 38° and 40° C. these effects became greater for both stratified and non-stratified seed, until at 42° C. no germination occurred. It is suggested that thiourea acts as a catalyst both to produce and break dormancy.

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