The Effects of Moist-Heat Treatments and Stratification on Germination of Prairie Plant Seeds

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THE EFFECTS OF MOIST-HEAT TREATMENTS AND STRATIFICATION
ON GERMINATION OF PRAIRIE PLANT SEEDS

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Abstract. Germination of Silphium terebinthenaceum was enhanced by a post-stratification moist-heat treatment at 80°C. Tested seeds of four other perennial herbs common to midwestern prairies (Andropogon scoparius, Sorghastrum nutans, Eryngium yuccifolium, and Solidago rigida) showed little adverse or beneficial effects of the heat treatment. Heat treatments alone had little effect on the seeds; the length of stratification periods necessary to effect maximal germination varied. The significance of these findings is examined in the light of related literature on grassland fire ecology.
INTRODUCTION

Despite the recent upsurge of research activity in the area of fire ecology, there has been very little work done with such basic units as the seeds of prairie plants since Blake's (1935) monograph. No work dealing directly with the effect of fire or artificial sources of heat on the percent or rate of germination of seeds of any of the dominant prairie plants was found in the extensive literature search conducted for this present work.

Much of the classical work in fire ecology has dealt with the gross effects of fire on woody plants or descriptions of conditions during and after forest fires (Ahlgren and Ahlgren, 1960; Biswell, 1963; Garren, 1943; Little and Moore, 1949), and use of fire in land management. A large part of the recent work with grassland fires falls into the last category. Wright's (1931) work, Stone and Juhren (1951), and Went et al. (1952) are among the few papers dealing with the effect of fire on seed, and these deal again with woody plants. Martin and Cushwa (1966) and Cushwa, Martin, and Miller (1968) present the results of subjecting seeds of Cassia nictitans to moist-heat treatments and also their comment on the lack of reports dealing with effects of fire on seeds of herbaceous plants.
FOREST AND GRASSLAND FIRES COMPARED

Cursory examination of the literature is sufficient to show that forest fire and grassland fire must be considered separately. The highest naturally occurring temperatures reported in grass fires, 798°C, was recorded during a spring fire on a Miscanthus type grassland by Iwanami (1969). Even at that high temperature, the temperature at the soil surface only reached a maximum of 187°C. Forest fires, on the other hand, commonly produce temperatures around 1150°C and maintain these extremes for relatively long periods (Daubenmire, 1968).

Secondly, most herbs are adapted to survive fire whereas most trees are killed by fire. Most perennating buds and seeds lie just at or below the ground surface, which remains quite cool as the flames pass. Because grass fires are characterized by a rather narrow zone of flames, any high temperatures produced are of short duration, on the order of 5 minutes.

Third, much of the material consumed in a grass fire is already dead; there is little material analogous to the extensive array of supporting tissue in a woody plant. Thus there is much less wastage of energy to the herbaceous plant.

Fourth, in addition to putting the herbaceous plant at less of a direct disadvantage, the less intense fire is not able to modify the soil as severely or as deeply as a forest fire.

Finally, only a very short time elapses before herba-
ceous plants redevelop normal ground cover. This means that there is far less time available for foreign seeds and fauna to take advantage of the drastically altered microclimates to establish themselves. Many months or years may pass before pre-burn conditions are restored following a forest fire.

Grassland fires themselves show a great variation depending on these three classes of factors: (1) weather conditions leading up to and prevailing at the time of the burning; (2) topographic conditions; (3) the kind, amount, and disposition of the fuel accumulated since the last fire (Daubenmire, 1968).

THE PRAIRIE AS A FIRE-MAINTAINED COMMUNITY

Prairies are often referred to as fire-maintained communities. It is indeed true that woody plants incapable of sprouting from their roots after a fire may be eliminated or reduced by a fire. This fact is employed in burning of range and pastureland. But grasses are favored over forbs only part of the time (Kucera and Kelling, 1964; Penfound and Kelting, 1950). In other cases, forbs were favored over annual grasses (Bently and Fenner, 1958; Biswell, 1956) and over perennial grasses (Daubenmire, 1968). It is obvious that the effects of fire on grasslands do not yield to simplistic generalizations, but that the effects depend on the composition of the community.
DESCRIPTION OF A GRASS FIRE AND ITS EFFECTS

Figure 1 shows an idealized flame as it passes the viewer standing to one side. There are four steps to the combustion of fuel. As the flame approaches, the fuel is preheated by radiation from the headfire, convection, and, to a much lesser extent, conduction. The second phase is endothermic decomposition, during which flammable and non-flammable gases are released. The third stage of combustion is the exothermic decomposition; this is the flaming stage. Finally, after the flames pass over a given region, the charred fuel continues to release energy in glowing or charcoal combustion (Martin et al., 1969).

In a grass fire the first three phases are very short in duration and there is little, if any, charcoal combustion. The portion of the fuel consumed by the fire, the available fuel, depends greatly on moisture content. The remaining fuel is termed the residual fuel.

Average temperatures and durations of these temperatures have been reported by several investigators. Iwanami and Iizumi (1969) measured maxima of 500°C at 8 cm elevation, an increase of 25-55°C at the soil surface, and no appreciable change 2-4 cm into the soil during a Miscanthus type fire. Iwanami and Iizumi (1966) reported soil surface temperatures not exceeding 91°C, with readings over 50°C maintained for only 151 sec during a Zoisie type fire.

Lawrence (1966) in a paper on chaparral fires, reported a maximum of 288°C was attained at the soil surface, while
the temperature at a depth of 2.5 cm reached only 82°C. Temperature at the soil surface ranged from 93-121°C depending on the amount of litter, in fires of annual grasses in California (Daubenmire, 1968). Temperatures at depths of 25, 51, 76, and 100 mm were 82, 74, 63, and 57°C respectively.

Somewhat higher temperatures with equally short durations were measured during fires in heather and other dwarf-shrub and grassland communities (Gimingham, 1971; Whittaker, 1961; Kenworthy, 1963; Kayll, 1966; Hopkins, 1965).

The possible effects of a fire on the flora of a community may be placed in four categories: (1) manipulation of growing conditions involving physical changes in the seedbed; (2) a chemical change in the environment of the plant or seed; (3) a change in the biotic environment; (4) a direct effect on the seed (Cushwa et al., 1968). Most work with grassland fires appears to operate on the premise that the major effects of fire are in the third category, with the elements of categories (2), (1), and (4) playing lesser roles.

For example, Stone (1951) observed a marked increase in flowering of some plants following a burn, which he attributed to an increase in light intensity at lower levels. Vogl (1964) reported that fire stimulated resprouting and early spring growth, increased the height of herbaceous growth, and increased flower, fruit, and seed stalk production. He attributed these results to the removal of the heavy layer of litter and production of fertilizing ashes. Komarek (1971) showed that litter is oxidized to a fertilizing ash rich in calcium, phosphate, and potassium. He also noted
that burning may quite literally cleanse an area of potential disease-causing organisms and insect pests. Pase (1971), on the other hand, reported no overwhelming adverse or stimulatory effect from an early spring burn of *Eragrostis lehmanniana*.

Went et al. (1952) nearly went so far as to eliminate any possibility of a direct effect of heat on the seeds of chaparral, saying instead that the major cause of the abundant germination in the first season following a fire was the removal of competing plants.

**THE EFFECT OF HEAT ON SEEDS**

There seems to be an almost universally held, if unquantified and unpublished, opinion that, aside from a few special cases such as strobili which must be opened by the heat of fire; high temperatures can only harm seeds, especially if they are not dry. There is a growing body of evidence, however, that suggests that many seeds may be adapted to resist injury by or even benefit from the heat of fire.

The only readily available data on the response of seeds of an herbaceous plant to heat treatments is contained in papers by Martin and Cushwa (1966) and Cushwa et al. (1968). Using *Cassia nictitans* (Caesalpiniaceae), these investigators showed that both rate and total percent germination were increased by giving the seeds moist-heat treatments. Without any stratification period, seeds heated at 80°C for various times up to 16 min germinated up to 95%, while controls
showed only a 12% germination. But *C. fasciculata* showed only a maximum of 3% germination regardless of the treatment.

Similar results have been reported for certain woody plants such as *Rhus ovata* (Stone and Juhren, 1951), *Kalmia hirsuta* (Jaynes, 1968), and *Calluna vulgaris* (Gimingham, 1971; Whittaker and Gimingham, 1962). On the other hand, Sweeney (1967) states that when the moisture level of seeds is over 30% higher than the moisture content of air-dry seeds, they may be killed by exposure to 80°C temperatures.

Cushwa *et al.* (1968) also report the results of moist-heat treatments on several species of *Desmodium* and *Lespedeza* and on *Galactia volubilis*, all of which are common to the fire ecosystems of the southeastern U. S. Only *L. bicolor* showed a significant and consistent improvement in the total percent germination; the others showed little effect in either direction.

The question thus arises as to the effect of moist-heat treatments on the germination of the seeds of plants common to our prairie grasslands. None of Blake's numerous treatments consistently produced a very respectable percentage of germination. Her explanation was that prairie herbs produce large numbers of seeds, of which only a small portion are viable. Perhaps what is required is the heat of a fire to produce better germination.
MATERIALS AND METHODS

Collection of seeds. Seeds of five perennial prairie herbs, Andropogon scoparius Michx. and Sorghastrum nutans (L.) Nash. of the Gramineae, Eryngium yuccifolium Michx. of the Umbelliferae, and Solidago rigida L. and Silphium terebinthenaceum Jacq. of the Compositae, were collected from plants in a prairie relict on the west side of the Penn Central Railroad tracks near Pokagon, Cass County, Michigan (NW 1/4, Sec. 33, T.6S., R.16W.; Pokagon Township) in October, 1970. They were stored under low to moderate humidity at 21°C for one year prior to use.

Approximately homogeneous batches of seeds were selected from those collected; seeds obviously damaged by insects were rejected as were conspicuously undersize or oversize seeds.

Cold treatments. Seeds were wrapped in moist Armstrong 6-in. filter paper and placed in small plastic bags. Four-, seven-, and ten-week periods at 2°C were used for stratification. An additional group was placed in a 2°C chamber for 2 weeks, removed to a freezer at -17.5°C for 6 weeks, and finally replaced in the 2°C chamber for 2 weeks. A control group received no stratification, the seeds being kept dry at 21°C.

The four- and seven-week stratification groups were omitted for the Silphium terebinthenaceum, since there were not enough seeds to complete all the treatments.

Heat treatments. Each group of seeds to be stratified for a
given length of time contained 450 seeds per species. Of these, 150 were given a heat treatment prior to stratification (fall fire simulation), 150 were heat treated after stratification (spring fire simulation), and 150 were given no heat treatment.

Treatments were performed on seeds which had imbibed for 4 hours in aerated, distilled water at room temperature. Heat treatments consisted of spreading the seeds out on moist Armstrong 6-in. filter paper, covering them with a second sheet of moist filter paper, and placing them in an oven preheated to 80°C. The seeds remained in the oven for exactly 5 min, during which time the temperature was held within a ±4°C tolerance.

Groups not being treated were soaked simultaneously in aerated, distilled water for 4 hours. While the other seeds were in the oven, they were spread out on Armstrong 6-in. filter paper and kept at 24°C.

All seeds were then returned to aerated, distilled water at room temperature for 2 hours.

Germination. Seeds were germinated in groups of fifty in 6-in. petri dishes on Armstrong 6-in. filter paper with 7.0 ml of distilled water added to each dish. In each group of 150, 50 were placed in a 16°C chamber, 50 were placed in a 21°C chamber, and 50 were placed in a 27°C chamber. All seeds were kept in complete darkness for the 14 days allowed for germination.

At the end of this period, percent germination in each
dish was calculated. A seed was determined to have germinated if any portion of the radicle had emerged by growth, not by mere swelling of the cotyledon(s) and subsequent cracking of the seed coat.

A flow diagram showing the overall procedure followed is shown in Figure 2.

Dates. The first groups of seeds were treated on October 18, 1971. The 7-week and 4-week stratification groups were treated on November 8 and 29, 1971, respectively. All seeds were germinated beginning December 27, 1971. The groups receiving no heat treatments and either being stratified for 10 weeks or being kept at 2°C for 2 weeks, -17.5°C for 6 weeks, and at 2°C for 2 weeks were repeated beginning on December 27, 1971. These seeds were germinated beginning on March 6, 1972.
RESULTS

It appears that only *E. yuccifolium* and *Silphium terebinthenaceum* were truly dormant according to Vegis' (1963) definition. The maximum germination of untreated seeds of the other four species was only 8%, however. Therefore, in practice, all seeds except those of *Sorghastrum nutans* were assumed to be dormant after a year of storage at 21°C.

The temperature most favorable for germination differed among the species tested. *Sorghastrum nutans* had no distinguishable optimum (Table 2). *E. yuccifolium* germinated much better at the two lower temperatures; in fact, some germination occurred before the end of the stratification period. In the 7-wks group, 5% of the seeds which had not been heat-treated germinated; this includes both controls and those seeds which were to be treated after stratification. In the 10-wks group, 10% of the seeds which had not been heat-treated germinated. In both the 7- and 10-wks groups, those seeds which had received a heat treatment showed an 8% germination (Table 1). *Solidago rigida* and *A. scoparius* germinated better at the two higher temperatures (Tables 3 and 4). Seeds of *Silphium terebinthenaceum* which were not heat-treated appeared to germinate better at the lower temperatures, while seeds receiving the post-stratification heat treatment germinated better at higher temperatures (Table 5).

Germination of seeds which had been frozen for 6 weeks did not exceed 12% in any of the species tested, and in over half of the groups, no germination occurred at all. Germi-
nation occurred in 40% of the controls, in only 26.6% of those groups receiving a pre-stratification heat treatment, and in 66.7% of those groups receiving a post-stratification heat treatment. In *Silphium terebinthenaceum*, the group of frozen seeds which received a post-stratification heat treatment germinated markedly better than the groups receiving no heat treatment or pre-stratification heat treatment (Table 5).

Cold stratification enhanced germination in all species. The length of stratification necessary to effect maximal germination varied. Viability of *E. yuccifolium* declined drastically after 7 weeks, viability of *A. scoparius* and *Sorghastrum* was about the same after 4, 7, or 10 weeks, and *Solidago rigidia* appeared to reach a maximum after about 7 weeks. No data was available for *Silphium terebinthenaceum*.

Heat treatments alone had little effect on breaking dormancy. Even in *Silphium terebinthenaceum* where germination was markedly enhanced by a heat treatment following 10 weeks of stratification, heat treatment without stratification caused a maximum of only 8% germination, while the corresponding control was 0% (Table 5).

Compared to corresponding groups receiving no heat treatment, pre-stratification heat treatments were, in general, inhibitory in that significantly lower germination occurred more often than significantly higher germination. This effect is perhaps most noticeable in *Sorghastrum nutans* (Table 2). Effects in the other four species were mixed.

Post-stratification heat treatments generally produced the opposite effect. At least marginally significant en-
hancement of germination occurred in *Sorghastrum nutans*, *Solidago rigida*, and *Silphium terebinthenaceum* (Tables 2, 3, and 5). Germination in *E. yuccifolium* may have been slightly depressed (Table 1).

**Fungi.** Since none of the seeds used were surface sterilized, the growth of mold on the germinating seeds presented a definite problem. The worst growth occurred on *Solidago rigida* and *Silphium terebinthenaceum*. *E. yuccifolium* had the lowest infection.
DISCUSSION

The cold and heat treatments were designed to simulate in idealized fashion, the actual physical conditions encountered by a seed of a prairie herb which was under the litter or buried in the upper few millimeters of the soil. Although snow would usually provide a temperature buffer so that the embryo would not be chilled to below freezing, sub-freezing temperatures are conceivable. Thus both cold, moist stratification and freezing were included. As pointed out in the introductory sections of this paper, extreme temperatures at the soil surface and in the first few millimeters of soil as a fire passes over a given point are usually quite low and of short duration. Also as the fire passes over, water from adjacent fuel layers or the product of the oxidation condenses around cooler objects, such as the seeds, buried in the soil or under the litter (Cushwa et al., 1968; Martin et al., 1969). Thus the seed will be subjected to moist heat. In lieu of steam heat treatments, imbibed seeds spread out between sheets of moistened filter paper were placed in an oven for 5 min at 80°C.

From the results it would appear that fire alone would be unable to effect germination of seeds on a prairie, cold stratification would still be required to give maximal germination. This cannot, however, be extended into an absolute, all-encompassing statement, for there are several qualifications.

First of all, there is obviously a great deal of varia-
tion among the species as regards the optimal temperature at which germination occurs. This is very seldom taken into account in viability testing, largely because of the extra labor involved in determining the optimum. Lack of optimal conditions, however, will produce an erroneous impression of the percent viability of the seeds in question.

Secondly, although there was no outstanding stimulation in four of the species tested, it may be significant that the heat treatments failed to exert a significantly adverse effect.

Third, the failure to obtain high germination might be due to the lack of some additional factor in the treatment regime the presence of which would permit expression of any beneficial effects, or may be caused by some unknown property of the seeds themselves. The possibility that the seeds require a longer period to germinate, for example, was raised by Blake (1935), who found that some seeds will germinate only after constant exposure to proper conditions for as long as six months. She also reported variations in viability between one year's seed and the next. For example, 37% of the *A. scoparius* collected in 1928 germinated, while other years' seed showed as little as 0.5% after the same treatment; *Solidago rigida* collected in 1929 gave 16.5% germination following exposure to actual winter conditions, while seeds collected in 1930 did not germinate after similar treatment. Sweeney (1967) raised an intriguing possibility in this connection. Seed polymorphism, that is, the existence of different types of seeds, some requiring scarification of some sort to germinate, others able to germinate without scarification, has
been demonstrated in *Astragalus congdonii*, *Trifolium ciliolatum*, and *Chenopodium album*. Production of a particular sort of seed might very likely be determined by the recentness of a fire. Future experiments might take this into account by using seeds collected over several growing seasons leading up to and following a fire or artificial burn.

Fourth, the viability of the numerous seeds produced by a prairie herb may indeed be low. If so, only by using large numbers of seeds or many multiples of test groups could small differences be identified as significant. Blake (1935) suggested that this was indeed the case. It is possible that there is an adaptive advantage in producing large numbers of non-viable seeds. The energy lost in doing this might be offset by the fact that, if insects or disease destroyed most of the seeds, an insignificant number of viable seeds, compared to the total number of seeds, would be destroyed. If less energy were required to make a non-viable seed, there would be a distinct advantage in producing many, largely non-viable seeds instead of fewer viable seeds.

Freezing was also ineffective as a dormancy breaker compared to cold stratification. Physical damage during thawing or denaturation of enzyme systems within the embryo probably outweigh any benefits derived from the treatment.

The positive results obtained from the post-stratification heat treatments, which supposedly simulate spring fires, lend credence to the idea that fire does indeed benefit the seeds of some prairie herbs. No pattern, such as forbs
benefitting and grasses being adversely effected, or vice versa, can be deduced, since each category included both positive and negative results. The mixed or negative results obtained from pre-stratification heat treatments may only be an artifact. If the germination mechanism was set in motion by the heat treatments only to be followed immediately by quiescence forced by cold stratification, a "confused" seed could result.
ACKNOWLEDGMENTS

The author gratefully acknowledges the cooperation of Dr. Leo C. VanderBeek and the advice of Dr. Richard D. Brewer, who suggested the experiment. Special thanks are also due to Mrs. Ann Stuurwold for helping to count the endless thousands of seeds.


Table 1. Percent germination of seeds of Eryngium yuccifolium as influenced by temperature, time of heat treatment, and length of stratification period. Where there were no longer 50 seeds per group because of germination during stratification, the numbers were rounded to the nearest even percent. Significant differences between values obtained for heat-treated seeds and corresponding controls according to the Chi-square test are indicated by the letter following the number, with a, b, c, and d referring to levels of $P<0.05$, 0.025, 0.01, and 0.005, respectively.

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Table 2. Percent germination of seeds of *Sorghastrum nutans* as influenced by temperature, time of heat treatment, and length of stratification period. Significant differences between values obtained for heat-treated seeds and corresponding controls according to the Chi-square test are indicated by the letter following the number, with a, b, c, and d referring to levels of $P < 0.05$, $0.025$, $0.01$, and $0.005$, respectively.

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Table 3. Percent germination of seeds of *Solidago rigida* as influenced by temperature, time of heat treatment, and length of stratification period. Significant differences between values obtained for heat-treated seeds and corresponding controls according to the Chi-square test are indicated by the letter following the number, with a, b, c, and d referring to levels of $P<0.05$, 0.025, 0.01, and 0.005, respectively.

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Table 4. Percent germination of seeds of *Andropogon scoparius* as influenced by temperature, time of heat treatment, and length of stratification period. Significant differences between values obtained for heat-treated seeds and corresponding controls according to the Chi-square test are indicated by the letter following the number, with a, b, c, and d referring to levels of $P<0.05$, 0.025, 0.01, and 0.005, respectively.

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Table 5. Percent germination of seeds of *Silphium terebinthenaceum* as influenced by temperature, time of heat treatments, and length of stratification period. Significant differences between values obtained for heat-treated seeds and corresponding controls according to the Chi-square test are indicated by the letter following the number, with a, b, c, and d referring to levels of P < 0.05, 0.025, 0.01, and 0.005, respectively.

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<th>Temp (°C)</th>
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<th>7 wks*</th>
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*treatments omitted because of lack of seed material*
FIGURE LEGENDS

Figure 1. The stages in the combustion of available fuel. Modified from Martin et al., 1969.

Figure 2. Flow diagram showing treatment of a group of seeds of a given species which were to be stratified for X weeks.
Figure 1

COOLING

CHARCOAL COMBUSTION

DISTILLATION AND COMBUSTION

PREHEATING

AVAILABLE FUEL

RESIDUAL FUEL

SOIL
Figure 2

450 SEEDS

150 "Fall Fire" SEEDS
- SOAKED 4 HRS
- HEAT-TREATED
- SOAKED 2 HRS
- STRATIFIED X WEEKS
- SOAKED 4 HRS
- KEPT MOIST AT 24°C
- SOAKED 2 HRS
- Stratified X WEEKS
- SOAKED 2 HRS
- Germinated
- 50 SEEDS
  16° 21° 27°

300 SEEDS
- SOAKED 4 HRS
- KEPT MOIST AT 24°C
- SOAKED 2 HRS
- STRATIFIED X WEEKS
- SOAKED 2 HRS
- Germinated
- 50 SEEDS
  16° 21° 27°

150 "Spring Fire" SEEDS
- SOAKED 4 HRS
- KEPT MOIST AT 24°C
- SOAKED 2 HRS
- Heat-treated
- SOAKED 2 HRS
- Germinated
- 50 SEEDS
  16° 21° 27°

150 "Controls" SEEDS
- SOAKED 4 HRS
- KEPT MOIST AT 24°C
- SOAKED 2 HRS
- Germinated
- 50 SEEDS
  16° 21° 27°