APPARENT HEAT STIMULATION OF BURIED SEEDS OF GERANIUM BICKNELLI ON JACK PINE SITES IN NORTHERN LOWER MICHIGAN*

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The germination of buried seeds is an important mechanism of species establishment during secondary plant succession in many ecosystems (Sweeney 1956, Major & Pyott 1966, Ahlgren 1979a, Hall & Swaine 1980, McGraw 1980). The appearance of a large variety of species, not seen on unburned areas, following fire has been attributed to stimulation of germination of buried seed (Went et al. 1952, Sweeney 1956, Floyd 1966, 1976, Christensen & Muller 1975a, Shea et al. 1979). Various factors resulting from fire have been implicated in this phenomenon. Went et al. (1952) reported that removal of competition was a major factor in the abundant germination of chaparral species the first season after fire. McPherson & Muller (1969) concluded that heat from fire degrades some substance in the soil which otherwise suppresses germination of chaparral species. The abundance of the annual Senecio sylvaticus on one-year-old burned Douglas-fir (Pseudotsuga menziesii) clearcuts and its disappearance thereafter have been attributed to soil nutrient changes associated with burning (West & Chilcote 1968). Rupture or alteration of the water-impermeable seed coat of hard-seeded species allowing germination has been attributed to fire (Floyd 1966, Cushwa et al. 1968, Martin et al. 1975, Purdie & Slatyer 1976, McDonough 1977).

Germination of many species is restricted to the first year after fire (Horton & Kaebebl 1955, Sweeney 1956, West & Chilcote 1968, Purdie & Slatyer 1976). On jack pine sites in northern lower Michigan, Abrams & Dickmann (1982) reported that many species on one-year-old burns were not present on the site the following year. The most striking example was Geranium bicknelli Britt., classified as an annual or biennial by Fernald (1950). This species represents as much as 22% of the vegetational cover on first-year burns, but by year two it was not present or was reduced to scattered individuals. It was hypothesized, therefore, that heat from fire was responsible for the appearance of this species on one-year-old burned sites.

In a preliminary experiment with freshly matured geranium seed pretreated with various combinations of moist heat and stratification, no unscarified seeds germinated. In contrast, 80 to 100% of seeds scarified by nicking the radicle-end with a razor blade germinated, regardless of pretreatment (Abrams 1982). These results suggested that if heat was involved in

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geranium germination, a period of dormancy in the soil was required before heat exposure was effective. To test this hypothesis, an experiment was initiated using soil samples collected from different-aged jack pine stands. The objective of this experiment was to determine if heat was involved in the germination of geranium seed buried in the forest floor. It was also possible to compare the germinants from buried seed with the existing flora of each site.

Three different-aged jack pine stands representing a post-fire successional sequence were selected for study: a clearcut area that had been prescribed burned 3 years previously, a 35-year-old post-fire jack pine stand and a 55-year-old jack pine stand of unknown origin. All stands were located in Ogemaw county in northern lower Michigan.

On May 12, 1981, 12 randomly located soil samples were collected from each site. The samples were 25 × 25 cm in area and 2.5 cm deep into mineral soil. The volume of each sample varied with the depth of the overlying organic material. Samples were bagged separately and air-dried in the laboratory until May 30, 1981. After removing all green vegetation, each sample was sifted through 60 mm mesh screening to remove larger twigs, roots, and rocks. Four treatments (unheated control, heated at 70°F for 30 min., heated at 90°F for 30 min., and heated at 70°C for 30 min. + stratification) replicated 3 times, were randomly assigned to 1352 cm³ subsamples taken from the screened soil samples from each site. Heated samples were placed in metal trays, moistened slightly, and placed in a forced-air drying oven. To raise samples to and maintain them at 70°C for 30 min., they were first exposed to 150°C for 20 min. (preheating), followed by heating at 100°C for 30 min. The 90°C for 30 min. treatment involved preheating samples at 180°C for 30 min. followed by heating at 120°C for 30 min. During the preheating, samples were periodically stirred and moistened throughout. No additional stirring or moistening was done during the final heating period. A thermometer was inserted into the center of each sample to monitor temperature during heating. In both the 70°C and 90°C heating regimes the samples remained moist through the final heating period.

All samples were next placed over a 3.5 cm layer of sterilized sand (autoclaved at 121°C for 60 min.) in 26 × 52 × 6.5 cm plastic flats. The samples were spread evenly over the sand to form a layer 1 cm deep. The flats designated for stratification were placed in refrigeration (1–2°C) for 8 weeks. All other flats were placed under “cool white” fluorescent lights in a completely randomized design. The flats were exposed to a 14 hour photoperiod with an approximate photonflux density of 35 microEinsteins m⁻² s⁻¹. Temperatures fluctuated between 20 and 25°C. Two flats containing only sterilized sand were used to detect possible contaminants to the experiment. The flats were systematically rotated once a week to reduce possible positional effects. Germination counts were made every two days for the first month and once or twice a week thereafter. After stratification was completed, those flats were placed under the light trays with the other flats. Samples were kept moist throughout the experiment by adding tap water every 1 to 2 days. During stratification, samples were watered every 7 to 10 days. Germinants were recorded as they appeared. Individuals not readily identifiable were removed, potted, and grown until they could be identified. The experiment was concluded after 18 weeks.

At the conclusion of the buried seed experiment, unheated control flats from the 3-year and 35-year-old sites were heated to 70°C for 30 min. using the above procedure to determine if geranium seeds in those flats would germinate when exposed to heat.

No seeds germinated in the flats containing only sterilized sand. However, three seedlings of Oxalis sp. came up in other flats and were considered contaminants; this species had not been found on any of the jack pine sites studied in northern lower Michigan.

Most of the germinants appeared during the first 2 weeks of the experiment (Fig. 1). A moderate amount of germination occurred from weeks 3 to 8 and very little thereafter, but there were differences among species (Fig. 2). Geranium germination peaked the first week but had concluded by the fourth week. A substantial number of grass seeds germinated during the second
Fig. 1. Cumulative and weekly number of germinants from the control, 70°C—30 min., and 90°C—30 min. treatments in 3-year-old, 35-year-old and 55-year-old sites (combined) during the buried seed experiment. Fig. 2. Weekly total number of germinants of geranium, grasses (all species combined), and hawkweed (Hieracium spp.) from control, 70°C—30 min., and 90°C—30 min. treatments in the 3-year-old, 35-year-old and 55-year-old sites (combined) during the buried seed experiment.

Peak germination of hawkweed (Hieracium spp.) occurred between weeks five and eight. When heated treatments (70°C, 90°C, and 70°C + stratification) are compared to the unheated controls at each site, striking differences in species composition and number of germinants are evident (Table 1). Most importantly, geranium seedlings appeared only in the heated treatments from
the 3- and 35-year-sites. Differences in the number of geranium germinants in the 90°C and 70°C + stratification treatment compared to the unheated controls were significant (P < .05) using Wilcoxon’s nonparametric two sample test (Steel & Torrie 1960). No seeds of geranium germinated in samples from the 55-year site.

Only a few seeds of grasses and sedges germinated in the heated treatments from any site. In contrast, 58 and 22 grass and sedge germinants were recorded in the control flats from the 35-year and 55-year sites, respectively. The differences in the number of grass and sedge germinants between the heated and control treatments from all sites were significant (P < .01) using Wilcoxon’s two sample test. Total number of germinants in treatments from each site ranged from 0 to 65, but these differences were not significant. However, the most frequently occurring species in each treatment from the sites differed. For example, 68% of the germinants from the 3-year site were geranium, whereas 71% of germinants on the 35-year site were grasses. Hawkweed, with 36 germinants, was the dominant species on the 55-year site. However, grass species and wintergreen (Gaultheria procumbens) also were important members of the buried seed pool on this site.

Many important members of the plant community observed on the sites did not appear as emergents from buried seed. Noteworthy was the scarcity of seedlings of Carex and absence of blueberry (Vaccinium spp.), both ubiquitous components of jack pine sites in northern lower Michigan. Also, many species that germinated from buried seed were not surveyed on the respective sites. Examples were wintergreen and Chimaphila umbellata (common pipsissewa) from the 3-year site; geranium, Antennaria neglecta (field pussytoes), wintergreen, Panicum capillare, and common pipsissewa from the 35-year site; and hawkweed, Viola adunca (hooked-spur violet), Danthonia spicata, Dichanthelium depauperatum, and Panicum capillare from the 55-year site.

When control flats from the 3-year and 35-year-old sites were heated, one flat from the 3-year site produced 7 geranium germinants and two flats from the 35-year site produced 2 and 3 geranium germinants.

Many chaparral species common to recently burned areas produce seeds which remain dormant in the soil between fires (Sweeney 1956, Christensen & Muller 1975b). Heat treatment has been shown to release seeds of several chaparral species from endogenously enforced dormancy (Stone & Juhen 1951, Sweeney 1956, Christensen & Muller 1975a, 1975b). Consistent with geranium germination in this study, germination of buried seed of certain chaparral species occurs after heating soil samples, whereas freshly matured seed does not germinate after heat treatment (McPherson & Muller 1969, Christensen & Muller 1975a). Christensen & Muller (1975a) speculated that germination of these species may be dependent on the gradual deterioration of seed tissue imposing mechanical restriction of the embryo. Dormancy of seeds stored in the soil for long periods may also result from chemical inhibition by neighboring vegetation. Researchers suggest fire removes the source of toxins (e.g. shrub foliage) and denatures residual chemicals in the soil, thereby allowing increased germination of many species (Muller et al. 1968, McPherson & Muller 1969, Christensen & Muller 1975a, 1975b).
TABLE 1. Total number of germinants for species appearing in soil samples from the 3-year, 35-year-, and 55-year-old post-fire sites during the buried seed experiment. Treatments were an unheated control, 70°C—30 min, 90°C—30 min, and 70°C—30 min + stratification.

<table>
<thead>
<tr>
<th>Species</th>
<th>3-year</th>
<th>35-year</th>
<th>55-year</th>
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<td>cont</td>
<td>70°C</td>
<td>90°C</td>
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<tr>
<td>Annual herbs</td>
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<tr>
<td>Geranium bicknellii</td>
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<td>23</td>
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<td>Fragaria virginiana</td>
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<td>Hieracium spp.¹</td>
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<td>9</td>
<td>1</td>
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<td>Viola adunca</td>
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<td>Woody perennials</td>
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<td>Chimaphila umbellata</td>
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<td>Gaultheria procumbens</td>
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<td>Grasses and sedges</td>
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<td>Carex spp.</td>
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<td>Danthonia spicata</td>
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<td>Dichanthelium depauperatum</td>
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<td>Oryzopsis pungens</td>
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<td>Panicum capillare</td>
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<td>Poa pratensis</td>
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<td>Unidentified grasses</td>
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<tr>
<td>Treatment totals</td>
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<td>21</td>
<td>37</td>
</tr>
</tbody>
</table>

¹Hieracium aurantiacum and H. venosum
However, abundant germination of many hard-seeded species following fire has been attributed directly to alteration of the seed coat by heat (Cushwa et al. 1968, Purdie & Slatyer 1976, Gill 1977).

Previous studies involving buried seed have generally found, as in this study, that there is very little correspondence between the buried seed pool and existing vegetation on the site (Oosting & Humphreys 1940, Donelan & Thompson 1980, Major & Pyott 1966). The absence of buried seed from woody dominants (e.g. blueberry in this study) has been documented (Major & Pyott 1966, Donelan & Thompson 1980). The absence of blueberry and the scarcity of Carex seedlings seen in this study may be due to these species reproducing mainly by vegetative means.

The appearance of Geranium bicknellii following fire (Ahlgren 1960, Ohmann & Grigal 1979, Outcalt & White 1981, Abrams & Dickmann 1982) and other disturbances such as cultivation, building removal, and road construction (Ahlgren, pers. comm.) has been documented in the Lake States. On jack pine sites in northern lower Michigan, peak occurrence of geranium is restricted to the first year after fire; individuals of this species are rarely present on older burned sites. This pattern of geranium behavior, however, does not occur on all Lake States sites. For example, Ahlgren (1979c) reported that G. bicknellii occurred in 90% of his sample plots two years after an old-growth red pine stand in northeastern Minnesota was burned. Krefting & Ahlgren (1974), also working in northeastern Minnesota, found geranium in 27% of the plots surveyed on a 4-year-old burn.

Ahlgren (1979a–c) extracted buried seeds in soil samples from many sites of different forest types and burning histories, and consistently found geranium to be an important component. Interestingly, when Ahlgren (1979c) monitored seedling emergence from intact soil blocks collected from a 270-year-old red pine stand burned 3 years previously and from an adjacent unburned area, geranium appeared only from the burned soil. Ahlgren (1979a) also planted soil-extracted geranium seed in sterile greenhouse soil and obtained 30% germination.

These data are in contrast to our findings. In Ahlgren’s experiments, no heat treatment was given to soil samples or soil extracted seed, yet the geranium seed germinated. In our experiments with buried seed, geranium germinated only in flats exposed to heat treatment. This was further substantiated when 3 of 6 unheated control flats from the 3-year and 35-year sites, which showed no geranium germination for 18 weeks, produced geranium seedlings after the soil was heated. Also, seeds extracted from bulk soil samples from the 3-year site showed 20% germination (37 seeds total) when heated to 90°C for 30 min., whereas no unheated seeds germinated (30 seeds total) (Abrams & Dickmann, unpubl.)

Geranium in Minnesota, in the field at least, does not require heat from fire for germination (Ahlgren, pers. comm.). The apparent heat requirement for geranium germination in northern lower Michigan suggests that ecotypic differences exist for this species.

SUMMARY: Geranium bicknellii dominates vegetative cover the first year after fire on many jack pine sites in northern lower Michigan, but in subsequent years it disappears. To test whether heat from fire was responsible for this behavior, experiments using seed buried in the soil of different aged jack pine sites were initiated. Germination of buried geranium seed only occurred in heated treatments from 3- and 35-year-old sites; unheated controls produced no
germinants. The apparent heat requirement for germination of buried geranium seed from sites in northern lower Michigan contrasts with other Lake States studies and suggests ecotypic differences in germination behavior.

Unheated soil from the 35- and 55-year-old sites produced significantly greater numbers of grass germinants than did heated treatments. Many important members of the plant community recorded on each site did not produce germinants in this experiment, and several species that germinated from buried seed were not surveyed on the sites.

LITERATURE CITED


Ahlgren, C. E. 1979c. Emergent seedlings on soil from burned and unburned red pine forest. ibid. 273, 3 pp.


REVIEW

ENDANGERED AND THREATENED PLANTS OF OHIO. Edited by Tom S. Cooperdrive.

Ohio Biological Survey Biological Notes No. 16. College of Biological Sciences, The Ohio State University, Columbus, Ohio 43210. 1983 [“1982”]. 92 pp. $10.00 postpaid.

Here is a concisely documented, thorough account of present knowledge concerning plants at risk—or even considered to be probably extirpated—in Ohio. It is an excellent model, carefully done, for such regional catalogs. The historical background and many bibliographic references will make it useful beyond Ohio for data on many of the most interesting plants of the Great Lakes region. Lichens, bryophytes, and vascular plants are included, but no algae or fungi. Records since 1950 are generally considered “recent” and in the absence of these a taxon will eventually be considered extirpated in the state if intensive field work in the near future does not relocate it.

Some species, such as Dalibarda repens and Besseya bulbii, are nearly as scarce in Michigan as in Ohio. On the other hand, many species which we take for granted as abundant elements of our aquatic and terrestrial vegetation are considered at least threatened in Ohio—a good illustration of the effects (sometimes combined) of more extensive impingement on “natural” sites and, inevitably, of different climates. For a few examples: Potamogeton gramineus, P. zosteriformis (and other species), Carex bebbii, C. trisperma, C. viridula, Juncus balticus, Clintonia borealis, Sarracenia purpurea, Drosera intermedia, Potentilla palustris, Rubus strigosus, Polygala paucifolia, Cornus canadensis, Pyrola secunda, Vaccinium myrtilloides, Menyanthes trifoliata, Melampyrum lineare, Linum boreale, and Campanula rotundifolia are all so widespread and common in Michigan that it comes as something of a shock to find them classed as threatened or even endangered in the state immediately to the south. The importance of state lists becomes obvious, and an excellent defense is presented for state criteria (rather than solely national ones) which reflect the “different problems and needs of conservationists, planners, and biologists at the state level. The identification of unique sites or unusual biological communities within our state is largely contingent upon the identification of their unusual component species. A state list offers greater resolution in determining priorities for management or protection."

Comparing statistics is also instructive. In Ohio, 196 vascular plants are listed as threatened, compared with 200 in Michigan. But 328 taxa of vascular plants are listed as endangered, including those considered probably or perhaps extirpated, while in Michigan we list 13 species as endangered plus 24 as presumed extirpated (though the latter are to be considered as threatened should they be rediscovered). Does Ohio truly have 25 times as many endangered species as Michigan, or have we been far more conservative in designating them?

An element of particular interest is those species especially characteristic of recently disturbed ground in northern Michigan. Of these, Polygonum ciliatum, Chenopodium capitatum, Geranium bicknellii, and Aralia hispida are all considered endangered in Ohio (the latter two may be extirpated) while Corydalis sempervirens is threatened. Such discrepancies in status for plants which, at least with us, depend on bulldozers to maintain ample habitat, suggest a topic for research, to be approached with great caution, on the biological requirements for survival.

E. G. Voss