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Ecology, Vol. 15, No. 4 (Oct., 1934), 364-373.

Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28193410%2915%3A4%3C364%3ATIOETW%3E2.0.CO%3B2-I

Ecology is currently published by The Ecological Society of America.

THE INFLUENCE OF EXPOSURE TO WINTER TEMPERATURES UPON SEED GERMINATION IN VARIOUS NATIVE AMERICAN PLANTS[1]

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It has long been known that the seeds of very many plants germinate best, and some only, after being exposed for a more or less protracted period to near-freezing temperatures, under conditions otherwise favorable to germination. Kinzel in particular ('26 and earlier papers) has studied the behavior of a large number of European species in this respect, while similar investigations have been carried on in this country by Rose ('19), Coville ('20), Adams ('27), Crocker ('30), and others. In the main, however, these American investigations have been undertaken from the physiological point of view or from that of the nurseryman and, with the exception of the paper by Adams, the number of native species which have been worked with is very small.

In view of this latter fact, and since information of this sort may possess considerable ecological value, it has seemed worth while to investigate the influence which exposure to winter temperatures has upon seed germination in a considerable number of native American plants. More especially the investigation was undertaken with a view to finding out whether there was any marked correlation between germination behavior in this respect and the geographical distribution of the plants concerned.

MATERIALS AND METHODS

Altogether, in the course of the four years (1927–1931) over which observations were conducted, more than 200 species were experimented with, many of these in two or three successive series. Seeds were collected, mostly by the writer, in various more or less widely separated and ecologically dissimilar localities (see list given below). Following its collection, all material was air-dried, and the seeds of fleshy fruits were usually, although not always, removed from the pulp. For experimental purposes, late in autumn the seeds were counted out in duplicate lots of mostly 100 or 200 each; or else, in the case of very tiny seeds difficult to count, they were measured out in duplicate lots of practically equal size by means of a specially made small glass measuring thimble. They were then planted in sterilized soil, in separate boxes made

[1] Contribution from the Osborn Botanical Laboratory and the University of Michigan Biological Station.

for the purpose. One box of each pair was placed out of doors in a cold frame for a refrigeration period of from 71 to 112 days (or, in one instance, 57 days), while the other box was kept in the greenhouse. In the indoor series, seedling counts were made at intervals of approximately a week for the first two months, and less frequently thereafter. The same procedure was followed with the outdoor boxes, when these latter were brought into the greenhouse at the expiration of the refrigeration period. Observations on individual seed series were continued in some cases for nearly a year and a half, all boxes being kept indoors during the second winter.

Observations and Discussion

Out of the mass of data accumulated in this way, the more essential facts are here presented in tabular form. Five groups of plants (tables I–V) have

Table I. *Seeds germinating only after a period of exposure to low temperatures*

	Number of seeds used	Number of seeds germinating	Number of days required for germination
Aconitum uncinatum (G)	100	34	(71) 21–35
Aralia nudicaulis (M)	100	24	(83) 246–395
Campanula rotundifolia, alpine form (A)	+	+	(71) 14–21
Caltha palustris (M)	100	5	(112) 35–48
Chiogenes hispidula (W)	+	147	(83) 35–98
Circaea alpina (M)	300	141	(83) 28–98
Clintonia borealis (M)	100	1	(83) 445
Cornus canadensis (C)	1000	109	(83) 35–150
Diapensia lapponica (A)	+	+	(83) 21–28
Eupatorium purpureum (S)	200	18	(71) 21–28
Euphrasia americana (C)	+	50	(71) 14–21
Gentiana andrewsii (S)	200	98	(83) 21–84
Iris prismatica (B)	100	45	(83) 21–35
Kalmia polifolia (M)	+	+	(71) 63–194
Lachnanthes tinctoria (B)	200	28	(71) 77
Lonicera oblongifolia (M)	100	9	(83) 21–70
Mikania scandens (G)	200	153	(71) 14–42
Polygonella articulata (M)	100	11	(83) 11–21
Pedicularis canadensis (M)	+	2	(112) 35–44
Pyrus americana (C)	100	9	(83) 25–49
Ribes prostratum (A)	100	26	(83) 21–49
Silene pennsylvanica (S)	200	55	(71) 14–21
Verbena stricta (Kansas)	200	109	(71) 14–63

been distinguished on a basis of the difference in the total number of seeds germinating in the refrigerated and non-refrigerated cultures respectively, as follows: (I) Seeds germinating only after a more or less protracted period of exposure to low temperatures; (II) Germination markedly higher (ratio 5:1 or more) in seeds exposed to low temperatures; (III) Germination distinctly higher (ratio greater than 2:1 but less than 5:1) in seeds exposed to low temperatures; (IV) Germination but little different (ratio between 2:1 and 1:2 inclusive) in refrigerated and unrefrigerated seeds; (V) Germination distinctly lower in refrigerated than in unrefrigerated seeds (ratio less than 1:2).

For the seeds listed in each table, the following data are presented in order: (1) Number, or quantity, of seeds used in each lot; (2) Number, or quantity, of seeds germinating (*a*) after refrigeration and (*b*) without refrigeration; (3) Number of days required for germination, both the number up to the time when first seedlings appeared and the number up to the time when last

TABLE II. *Germination markedly higher (ratio 5 : 1 or more) in seeds exposed to low temperatures*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Alnus crispa (A)	200	80	5	(71) 14–35	106–134
Alnus incana (S)	200	23	3	(112) 14–55	126
Alnus mollis (C)	200	71	4	(71) 14–35	76–153
Aletris farinosa (B)	+	+	±	(83) 35	252
Arenaria groenlandica (A)	+	+	±	(71) 14–35	13–69
Betula glandulosa var. *rotundifolia* (A)	200	49	7	(83) 14–28	27–299
Betula papyrifera (M)	200	73	16	(83) 21–56	27–252
Cassiope hypnoides (A)	+	+	±	(83) 21–28	78
Eupatorium rotundifolium (B)	200	12	2	(71) 28–42	106
Iris versicolor (S)	100	26	5	(71) 21–42	106–265
Kalmia angustifolia (B)	+	+	±	(83) 21–28	111–125
Kalmia latifolia (S)	+	+	±	(83) 42	125
Ledum groenlandicum (W)	+	+	±	(83) 21–28	97–111
Leiophyllum buxifolium (B)	+	+	±	(83) 98	252–298
Liatris graminifolia (B)	200	18	1	(83) 20–56	97
Loiseleuria procumbens (A)	+	+	±	(83) 21–28	97
Polygala polygama (M)					
Cleistogamous seeds	100	28	1	(83) 28–70	129
Non-cleistogamous seeds	100	17	3	(83) 21–49	90
Potentilla tridentata (A)	200	147	25	(71) 7–14	78–148
Prenanthes trifoliata, alpine form (A)	100	28	5	(83) 11–56	20–41
Prunus pumila (M)	45	8	1	(83) 21–35	420
Rhododendron canadense (C)	+	+	±	(83) 35	125
Rhododendron lapponicum (A)	+	+	±	(83) 21–28	83
Ribes cynosbati (M)	100	45	8	(83) 21–49	20–252
Sambucus canadensis (C)	100	57	5	(83) 25–70	55–330
Smilacina racemosa (M)	100	30	2	(112)264	376
Smilacina stellata (M)	100	50	7	(71)194–500	148–265
Solidago odora (S)	200	49	8	(83) 21–70	20–97
Tanacetum huronense (M)	200	118	24	(71) 7–42	64–92
Vaccinium uliginosum (A)	200	110	9	(83) 21–70	153–181
Vaccinium vitis-idaea (A, C)	400	147	12	(83) 28–169	252–299

seedlings were observed (*a*) after refrigeration and (*b*) without refrigeration. Also, preceding the figures for germination period in column 3*a*, in parenthesis is given the length of the refrigeration period (in days). The plus (+) sign in column 1 indicates that measured quantities and not counted lots of seed were used. The same symbol in columns 2*a* and 2*b* should be interpreted to mean "considerable germination"; the symbol "±" to mean

"more or less germination." In addition, the geographical source of seed is indicated in each case by a letter in parenthesis immediately following the species name, as follows: southern New England, wild (S); cultivated in Yale Botanical Garden (G); pine barrens of southern New Jersey (B); Maine coast, in vicinity of Penobscot Bay (C); lower slopes (W) and alpine summits (A) of White Mountains, New Hampshire; northern Michigan (M), in general vicinity of the University of Michigan Biological Station at Douglas Lake, Cheboygan County. Unless otherwise designated, the species names are those of Gray's Manual, seventh edition.

As had been anticipated, difficulty was experienced with many seeds in

TABLE III. *Germination distinctly higher (ratio greater than 2 : 1, but less than 5 : 1) in seeds exposed to low temperatures*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Aralia hispida (M)	100	8	3	(83) 98–400	125–181
Cornus amomum (S)	200	19	6	(83) 25–35	55–111
Draba arabisans (M)	+	467	106	(83) 11–49	13–48
Fragaria virginiana (M)	200	143	52	(83) 21–56	27–252
Gentiana crinita (S)	200	59	23	(83) 21–28	27–69
Ilex glabra (B)	100	12	3	(83) 277–395	252–511
Maianthemum canadense (M)	100	51	26	(83) 42–84	181–252
Nyssa sylvatica (S)	100	55	27	(71) 28–120	106–265
Pieris mariana (B)	+	208	48	(83) 21	48–111
Ranunculus septentrionalis (M)	200	87	34	(83) 21–49	55–90
Ribes hudsonianus (M)	100	65	25	(83) 21–49	20–167
Sabatia dodecandra (B)	+	170	78	(83) 25–49	48–69
Solidago cutleri (A)	200	151	67	(83) 11–70	20–167
Vaccinium caespitosum (A)	200	66	18	(83) 28–169	83–252
Vaccinium pennsylvanicum (M)	200	103	42	(83) 28–169	48–139
Vaccinium pennsylvanicum var. *nigrum* (M)	200	61	21	(83) 35–169	48–252

securing adequate germination, under the conditions of the experiment, and in a considerable number of cases there was no germination at all. It has not seemed worth while to list these latter. Failure to germinate in some instances was manifestly due to immaturity or infertility of material at the time of collection; in others to the short viability of the seeds or to their inability to survive dessication; in others to the great length of time required for afterripening. In still others the causes remain to be determined. Brief reference may be made to a few suggestive examples. (1) Seeds of *Dirca palustris,* ripening in June and demonstrated by cutting to be fertile, were planted immediately. At the end of three months there had been no germination, yet all that remained was the empty seed coats. (2) Seeds of *Prunus pennsylvanica* treated in the usual way showed no germination whatever at the end of 17 months in either refrigerated or non-refrigerated boxes, although the

embryos were still sound. It was suggested that this might be one of those seeds which normally germinate only after passing through the digestive tract of some bird; but experiment failed to confirm this idea. Two hundred seeds from cherries which had been eaten and ejected by a captive cedar waxwing or " cherry bird " were planted in two lots, one refrigerated and the other not. Only four of these germinated. On the other hand, 200 seeds in which the bony outer seed coats had been clipped off at one end, so as to expose the

TABLE IV. *Germination but little different (ratio between 2 : 1 and 1 : 2 inclusive) in refrigerated and unrefrigerated seeds*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Anemone canadensis (M)	200	34	29	(71) 35–49	64–78
Anemone cylindrica (M)	100	10	9	(83) 169–308	90–330
Anemone multifida (M)	200	86	80	(83) 21–49	27–90
Aquilegia canadensis (M)	400	339	234	(83) 21–56	27–90
Antennaria neodioica (M)	+	+	+	(83) 11–21	13–90
Arisaema triphyllum (S)	100	79	82	(71) 21–63	34–92
Arnica mollis (A)	200	3	5	(83) 28	20
Asclepias tuberosa (G)	100	90	46	(71) 21–49	34–134
Aster novae-angliae (G)	200	129	123	(71) 14–28	43–78
Baptisia tinctoria (S)	70	54	69	(112) 14–217	51–329
Campanula rotundifolia (M)	+	+	+	(83) 11–28	13–69
Cassia chamaecrista (B)	100	20	18	(71) 14–77	15–148
Cercis canadensis (Tenn.)	100	2	1	(83) 25	167–181
Chrysopsis mariana (B)	200	80	44	(83) 11–70	41–90
Cirsium hillii (M)	50	36	26	(83) 11–98	13–41
Cirsium muticum (S)	200	16	16	(83) 21–42	29–299
Cirsium pitcheri (M)	200	169	97	(71) 7–28	13–69
Coreopsis lanceolata (M)	100	62	90	(112) 14–217	90–329
Cornus circinata (M)	100	26	45	(83) 98–654	83–520
Cornus stolonifera (M)	100	25	14	(83) 21–277	252–510
Corydalis glauca (S)	100	47	45	(83) 21–42	20–21
Elymus arenarius (C)	100	78	51	(83) 11–28	13–69
Empetrum nigrum (A)	100	3	2	(83) 169	299
Epilobium angustifolium (C)	+	938	658	(83) 11	13
Fragaria vesca (M)	200	91	64	(83) 14–56	48–252
Gentiana porphyrio (B)	+	100	50	(71) 14–21	43
Geum peckii (A)	300	22	14	(83) 11–42	34–83
Geum rivale (M)	300	70	83	(83) 14–35	20–90
Geum strictum (M)	300	211	152	(83) 11–35	13–41

embryo, gave 35 per cent germination within two weeks after being brought into the greenhouse, and 42 per cent within a month, following 4 months refrigeration out-of-doors; while another lot, similarly clipped but planted in the greenhouse, gave no germination within 6 weeks, at the end of which time only the empty seed coats remained. (3) Seeds of *Taxus canadensis* and *Clintonia borealis* were still sound at the end of 21 months in both refrigerated and unrefrigerated material; but the only sign of germination was a single

Clintonia seedling which had appeared during the seventeenth month. (4) Seeds of *Myrica gale* collected in April, after they had been on the bushes all winter, gave germination results which were very different from those given by seeds collected in August (see table V), as follows:

(*a*) 200 seeds sown on wet filter paper in petri dishes and placed in west window, where exposed to afternoon sunlight, gave 41 per cent germination in 3 weeks and a total of 43 per cent in 5 weeks.

TABLE IV—*continued*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Helianthus angustifolius (B)	200	32	24	(71) 21–42	64–106
Houstonia caerulea var. *faxonii* (A)	200	150	157	(71) 28	22–120
Linnaea borealis (M)	200	44	57	(71) 28–49	76–273
Lithospermum gmelini (M)	50	3	4	(83) 25–84	34–139
Lobelia cardinalis (S)	+	366	219	(83) 21–98	27–90
Lonicera canadensis (M)	100	111(!)	98	(83) 35–84	34–90
Lonicera dioica (M)	100	93	93	(83) 42–98	34–111
Lonicera hirsuta (M)	100	43	43	(83) 70–169	41–97
Lophiola aurea (B)	+	±	±	(83) 42–84	90
Lupinus perennis (S)	100	41	41	(71) 7–63	15–106
Mitella nuda (M)	200	125	84	(83) 64–98	48–139
Nemopanthus mucronata (M)	100	14	28	(83) 338–565	252–511
Phyllodoce caerulea (A)	+	+	+	(83) 21–28	83–125
Phytolacca decandra (S)	100	85	61	(71) 21–77	64–265
Rhamnus alnifolia (M)	200	82	78	(83) 28–390	41–474
Ribes tristis (M)	100	69	73	(83) 169–277	41–125
Sarracenia purpurea (B)	200	16	13	(71) 42–49	64–120
Senecio aureus (M)	50	50	46	(83) 11–35	13–41
Senecio balsamitae (M)	200	180	190	(83) 11–98	13–83
Shepherdia canadensis (M)	100	14	14	(83) 11–21	252–511
Solidago macrophylla (W)	100	50	39	(83) 11–21	13–167
Ulmus serotina (Tenn.)	100	46	26	(83) 21–42	90–181
Vaccinium canadense (M)	200	21	22	(83) 35–169	111–252
Vaccinium corymbosum (S)	200	89	106	(83) 49–216	41–252
Vernonia noveboracense (S)	100	78	57	(83) 11–21	34–90
Viburnum nudum (B)	100	58	72	(71) 63–194	92–148
Viburnum opulus var. *americanum* (W)	100	71	72	(112) 62–217	153–329

(*b*) 200 seeds sown as above but placed in dark cupboard showed no germination at the end of 3 weeks; and thereafter only 11 per cent during the 6 weeks following their transfer to a position alongside *a*.

(*c*) 200 seeds sown as above but refrigerated for 4 weeks at 5° C. gave 54 per cent germination within 3 weeks after being placed alongside *a*, with a total of 58 per cent in 5 weeks.

(*d*) 300 seeds sown on moist earth in glass-covered pot and place outside north window gave 29 per cent germination in 3 weeks and a total of 40 per cent in 6 weeks.

(*e*) 300 seeds treated as in *d* and placed alongside, but covered with blackened glass, gave a germination of only 1 per cent in 3½ weeks and none thereafter during a total period of 8 weeks.

Considered as a factor of ecological importance in relation to the northward geographical distribution of plants, it is obvious that there are two ways in which seed exposure to low winter temperatures may influence germination behavior in the plants concerned. It may influence the proportion of fertile seeds which will germinate, resulting in either an increased or decreased number of seedlings, as compared with seeds not so exposed; it may influence the length of the germination period, both the number of days before germination

TABLE V. *Germination distinctly lower in seeds which have been exposed to low temperatures (less than 1 : 2)*

	Number of seeds used	Number of seeds germinating		Number of days required for germination	
		After refrig.	Without refrig.	After refrig.	Without refrig.
Alnus rugosa (S)	200	26	62	(83) 25–70	48–111
Arenaria stricta (M)	+	1	14	(83) 185	13–83
Eryngium aquaticum (B)	200	10	76	(71) 42–49	27–90
Gaylussacia baccata (M)	200	13	44	(83) 42–169	111–330
Gaylussacia frondosa (B)	200	3	13	(83) 169–550	125–511
Lathyrus maritimus (M)	100	3	8	(83) 21–84	13–27
Magnolia grandiflora L. (Tenn.)	100	0	35	—	90
Magnolia virginiana (B)	100	3	15	(83) 169–440	78–420
Mitella diphylla (M)	200	37	134	(83) 35–98	41–69
Myrica carolinensis (S)	100	2	13	(71) 77	106–148
Myrica gale (M)	100	1	11	(83) 247	83–330
Rubus idaeus var. *canadensis* (M)	100	26	60	(83) 98–169	90–390
Sambucus racemosa (M)	100	11	51	(83) 70–169	139–252
Trientalis americana (M)	200	0	73	—	111–181
Viburnum alnifolium (W)	100	26	60	(83) 84–307	69–330
Viburnum cassinoides (M)	100	6	23	(112) 70–217	207–376
Viburnum dentatum (S)	100	8	65	(83) 397–427	391–511

begins and the length of time over which germination, once started, continues. The first effect is the one with reference to which the plants studied have been grouped in tables I–V; but the second effect may be equally important. As will be seen from examination of the tables, exposure to low winter temperatures ordinarily results in a shortening of the germination period, which in many cases is very pronounced. Such an effect may be of great ecological importance to plants of northward distribution, since it enables them to make the most of a relatively short growing season. The behavior of *Shepherdia canadensis* (table IV) in this respect is particularly striking. In this plant no difference whatever was found in the number of seeds germinating, but there was a remarkable difference in the length of the germination period in the two cultures, namely 11–21 days for refrigerated seeds as compared with 251–511 days for seeds which had not been so treated.

Crocker has shown, for a considerable number of plants which are important in nursery practise, that there is not only a "best temperature" at which different seeds should be stratified previous to germination, but also a "best time" for which this treatment should be continued. With regard to the behavior of native wild plants in this respect, the present experiments are not conclusive. Evidence in favor of a "best time" is suggested by the germination behavior of 18 species which were refrigerated in duplicate lots for 71 and 83 days respectively. In 44 per cent of these cases the seeds exposed to the shorter refrigeration period germinated more quickly and in 39 per cent, those exposed to the longer period; but in 17 per cent there was no difference. Corresponding figures for 16 species in which the seeds were refrigerated for 83 and 112 days, respectively, were 25, 44 and 31 per cent; for 4 species refrigerated 71 and 112 days, they were 25, 25 and 50 per cent. The germination behavior in *Cornus canadensis* is even less conclusive.

Seeds	refrigerated	57	days	germinated	11	per	cent	in	68–82	days
"	"	83	"	"	4	"	"	"	35–42	"
Fruits	"	57	"	"	23	"	"	"	61–96	"
"	"	83	"	"	5	"	"	"	150	"
"	"	112	"	"	10	"	"	"	35–83	"

In comparing rapidity of seed germination as affected by length of preliminary exposure to cold, the fact may be significant that, with all three of the refrigeration periods used, the subsequent germination period was essentially identical. Thus the average number of days which elapsed between the time cultures were brought into greenhouse and the appearance of first seedlings was 21 for 46 species which had been refrigerated 71 days and 22 both for 82 species which had been refrigerated 83 days and for 20 species which had been refrigerated 112 days. These figures are for species in which germination started in less than 50 days and are of known application only within the refrigeration limits here employed.

Incidentally, among the numerous features of detailed behavior which were noted among the various individual species dealt with, there is one which stands out as being of unusual interest. Two sets of *Campanula rotundifolia* seeds were collected, the first in 1928 from normal vigorous plants, a foot or more in height, growing among the sand dunes along the Straits of Mackinac in northern Michigan; the second in 1929 from dwarf alpine plants, less than 6 inches high, growing above timber line, at an elevation of about 5000 feet, in the White Mountains. The station for the latter, situated a short distance east of the Appalachian Mountain Club "Lake of the Clouds Hut," in all probability is the same "stony alpine moor on Mount Monroe" from which Tuckerman (1843) described his "variety *alpina*" of this species. Seeds from the lowland plants germinated abundantly in both refrigerated and unrefrigerated cultures, in the ratio of about 5 to 3; while seeds from the alpine

plants germinated abundantly in the refrigerated culture but not at all in the other. But this is not all. Seedlings of both forms were transplanted to outdoor conditions in the Yale Botanical Garden, where they have now been growing side by side, under ordinary garden conditions, for three years. The offspring of the lowland plants, as was expected, resemble their progenitors; but so also do the offspring of the alpine forms which for three summers now, while occasionally sending up a somewhat taller shoot, on the whole have maintained the dwarf habit of their parents.

Examination of the tables reveals puzzling discrepencies in the germination behavior of a number of species. How far these represent the effect of differences in environment and how far they are due to chance or to faulty technique is a question which must be left for future investigations to decide. By and large, among those plants of northward distribution which were studied there can be no question as to the advantageous influence of winter refrigeration in stimulating seed germination, while a similar relation seems to hold for many plants of southward distribution. A more extended study of some few carefully selected examples of both northern and southern plants with reference, among other things, to optimum refrigeration temperatures and times, would be well worth while. To others who may contemplate such studies it is suggested that the petri dish method, as used by Kinzel and others, is distinctly preferable to the soil culture method used by the writer; that results will be more conclusive if much larger numbers of seeds are employed; that presence and absence of light should be taken into account as possible determining factors; that provision should be made for continuing observations, when necessary, over a period of several years.

Summary

1. The influence upon seed germination of exposure to winter temperatures was studied in a large number of native eastern American plants, mostly species of northward distribution.

2. Tables are presented showing the germination behavior of seeds in 141 species, both after exposure and when not exposed, figures being given in each case for number of seeds used, number of seeds germinating, and number of days required for germination.

3. The conclusion is reached that winter refrigeration of seeds, in its effect both upon the number germinating and upon the length of the germination period, may be an ecological factor of much importance in relation to the northward distribution of plants.

4. Attention is called to the persistence of the dwarf habit of their parents in plants of *Campanula rotundifolia* which were grown from seed produced by the alpine form of this species, growing on Mount Monroe, in the White Mountains.

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