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STUDIES ON THE GERMINATION OF SEEDS OF COLORADO ALPINE PLANTS

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INTRODUCTION

Studies were begun in the fall of 1960 on the germination of seeds of a number of species of plants from the alpine areas of the Front Range of the Rocky Mountains of Colorado. These alpine, or tundra, areas occur on ridges and peaks that extend above the tree-limit, which is found at a general level of 11,400 feet (Marr, 1961). The tundra in Colorado is the most extensive of such areas found in any state other than Alaska, comprising $31\frac{1}{2}\%$ of the state's surface area (Schwan and Costello, 1951).

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The vegetation of the alpine is composed largely of short perennial grasses, sedges, herbs, and dwarf shrubs, which form a mat-like or cushion-like ground cover. Plants several decimeters in height may occur in protected areas or under favorable moisture conditions, however. Local ecological conditions are quite variable, and the vegetation also varies greatly with differences in exposure to sun and wind, with soil and moisture conditions, with depth and duration of snow cover, with frost action, and with pocket gopher activity (Osburn, 1958). The heterogeneous assemblage of habitats making up the alpine regions provides growing sites for more than 150 species of flowering herbs and small shrubs in 28 families, in addition to approximately 75 species of sedges, grasses, and rushes. These species are more or less restricted in Colorado to the tundra.

The present studies were devoted to determining the germinability over several years' time of the stored seeds of 18 species of flowering perennial herbs and one grass. Bliss (1958) tested seeds of 26 alpine species from Wyoming and 36 arctic species six to seven months after they were collected, and Steshenko (1963) has reported on germination studies with seeds of alpine plants from the Pamir Mountains of Russia. Tests with seeds of arctic species have been carried out by Söyrinki (1939) and Sørensen (1941). Little other information exists, however, on germination, viability, and dormancy problems with respect to seeds of alpine plants, and so the present studies were undertaken in preparation for other investigations on the physiological ecology of Colorado alpine plants.

MATERIALS AND METHODS

The seeds employed in the germination studies were collected when ripe from the parent plants in July, August, September, and October of 1960 and 1961, with most of the collecting being done in August. The seeds were secured from two localities in the Front Range of the Rocky Mountains of central Colorado: Summit Lake in Clear Creek County at an elevation of 12,834 feet and Rollins Pass in Boulder County at an elevation of 11,671 feet. These localities are both well above timberline, and the species utilized are common flowering perennials of the alpine tundra. Voucher specimens were collected and deposited in the herbarium of the University of Colorado Museum.

The seeds and other plant parts collected with them in the field were allowed to dry in paper bags on a laboratory shelf for several weeks, except when fresh seeds were germinated. The material was then screened to separate the seeds from the larger pieces of debris, and individual seeds were finally picked out by hand and placed in screw-top vials. Shrunken seeds or those appearing to

be damaged in any way were eliminated. The vials were stored in the laboratory at room temperature.

Germination tests were carried out under diffuse natural light conditions on laboratory shelves. The seeds were placed on two layers of filter paper moistened with distilled water in 15-cm. petri dishes. Water was periodically added to the dishes as required, with any excess being drained off. Daily records were kept of the percentage germination for each species in each test. The tests were continued for two weeks, and in most cases no further germination occurred in the last several days of the test, or else the germination had dropped to a negligible amount, except where noted below.

Since the seeds were generally difficult to secure in any great amount because of the small size of the alpine plants and their often scattered occurrence, and since the seed supply was purposefully conserved in order to permit monthly tests over as long a period as possible, only 50 seeds each of some species were used each month. Several replicates would have been desirable in these cases, of course, but the use of relatively small seed numbers made it possible to extend the tests over a period of several years, with a maximum of 38 months with one species. In some tests, however, it was possible to use four replicates of 50 seeds each. No attempt was made in this study to examine the possibility of dormancy in any of the species, and no special treatments other than those described were employed to increase germination.

The species names employed are according to Weber (1961), with the exception of *Melandrium furcatum*, which is there designated as *Lychnis kingii*. Fruits such as the achenes of members of the Polygonaceae and Compositae and the caryopses of the grasses are here treated as seeds.

RESULTS

The germination data on the species studied are presented in figures 1 through 11. The data for two series of tests with a single species were combined for comparison purposes into one figure, when seeds from the two different localities (Rollins Pass, RP, and Summit Lake, SL) were employed or when seeds from two different years were used. In the remaining figures the monthly germination percentages for two or three species were arbitrarily combined into one figure in each case. Tests were initiated at the beginning of each month indicated, except for the month of harvest, when seeds were germinated immediately after being collected, if tested at all that month.

Antennaria alpina (L.) Gaertn. (Figure 1): the seeds of this species were collected July 25, 1961, on Rollins Pass. They showed very low germination two months later when the tests were initiated on October 2. A gradual in-

crease in germinability is evident over the 22 months of the tests, a maximum of 60% being attained in the 20th month of testing (the 22nd month after harvest). There is evidence of germination "peaks" in the middle or early summer of both years of the tests, which may relate to generally higher room temperatures during the summer months when the tests were conducted. However, the rate of germination was not increased at these times.

Arenaria fendleri Gray (Figure 2): the seeds were collected August 25, 1961, on the east side of Summit Lake. Germination was almost complete from the time of the first test the following March, a little over six months following harvest, through the nineteenth month after harvest. Germination fell during the October test for unexplained reasons but rose again in the six months following.

Arenaria obtusiloba (Rydb.) Fern. (Figure 2): the seeds were collected October 8, 1960, on Rollins Pass and August 18, 1961, on the east side of Summit Lake. Germination percentages of seeds from the two locations and two seasons are compared. Tests with the 1960 seeds were begun in October immediately upon harvest, and germination was found to be low throughout the 31-month test period. A slight trend toward improved germinability after two years may perhaps be noted. Germination tests on the 1961 Summit Lake seeds were begun in March of 1962, about six months after harvest, and initial germination was high, with a gradual decline in germinability becoming evident after the first year and continuing until the tests were terminated 23 months after harvest. At all times the 1961 SL seeds germinated better than the 1960 RP seeds, however. Bliss (1958) found with small seed samples of this species that light improved germination somewhat over dark conditions. The germination percentage of his Wyoming seeds is comparable to those found in the present study with Summit Lake seeds.

Arenaria rubella (Wahl.) Sm. (Figure 3): the seeds were collected August 18, 1961, on the north side of Summit Lake and August 25, 1961, on Rollins Pass. Tests of seeds from both locations were begun in March of 1962, about six months after harvest. Initial germination in the SL seeds was high, but germination dropped to only 2% the following month and remained low until September, at which time a dramatic rise took place. Germination in the RP seeds was only 6% in the initial test and remained low through August. Fall and winter germination was relatively high, with a decline appearing again the second summer. The data suggest that in this species the higher temperatures in the laboratory during the summers are inhibitory to germination.

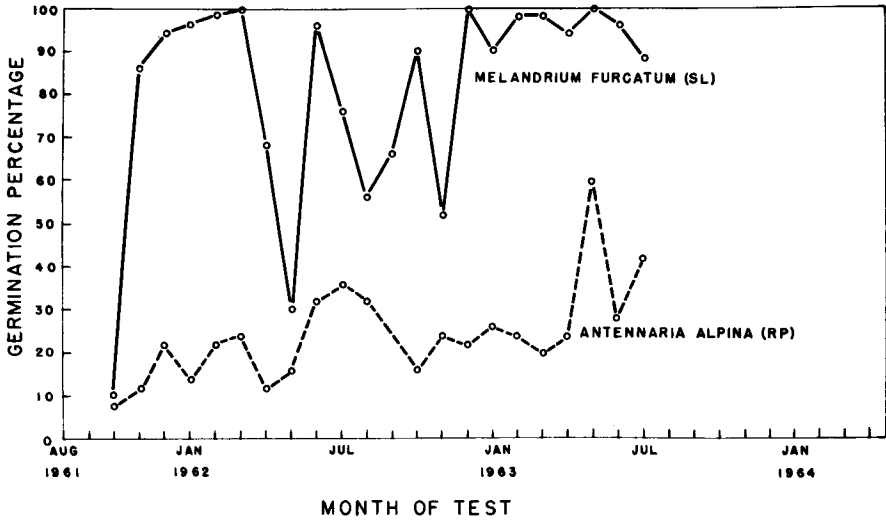


FIGURE 1.

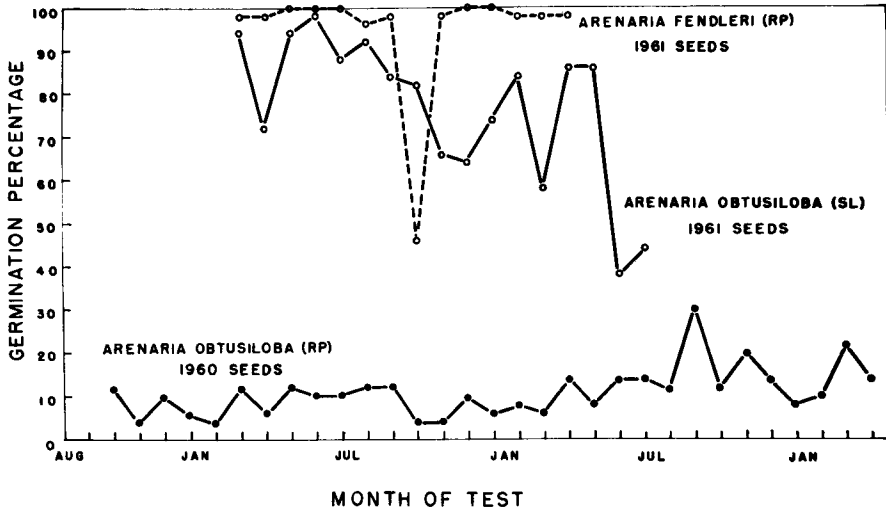


FIGURE 2.

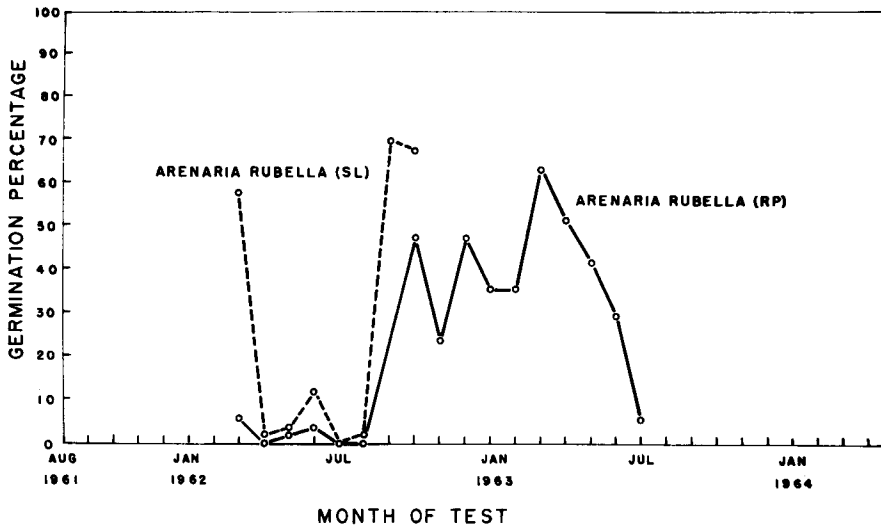


FIGURE 3.

Cerastium beeringianum C. & S. ssp. *earlei* (Rydb.) Hulten (Figure 4): the seeds were collected August 18, 1961, on Rollins Pass and September 1, 1961, on the east side of Summit Lake. Tests of the two seed lots were begun in October and continued for 21 months, with 200 seeds from Summit Lake being tested each month. Initial germination was low in both seed samples but rose to 85% in the SL seeds in four months and remained mostly high until a decline occurred in the last test. RP seeds exhibited low germinability for the entire first year but reached 90% the eighteenth month after harvest, with a final decline in the last months of testing.

Geum rossii (R. Br.) Ser. (Figure 5): the seeds were collected August 26, 1960, on Rollins Pass. The freshly-harvested seeds gave an initial germination of 32% and generally improved in germination during the 12 months of testing. Bliss noted an increase in germination in the light and found germination in a small seed sample to be somewhat better than that reported here.

Heuchera parvifolia Nutt. (Figure 6): the seeds were collected August 25, 1961, on Rollins Pass. Initial germination in October was good, and the percentage remained high during the first 20 months of testing but dropped in the twenty-first month and in the final twenty-second month. Two hundred seeds of this species were tested each month. Germination continued to a slight

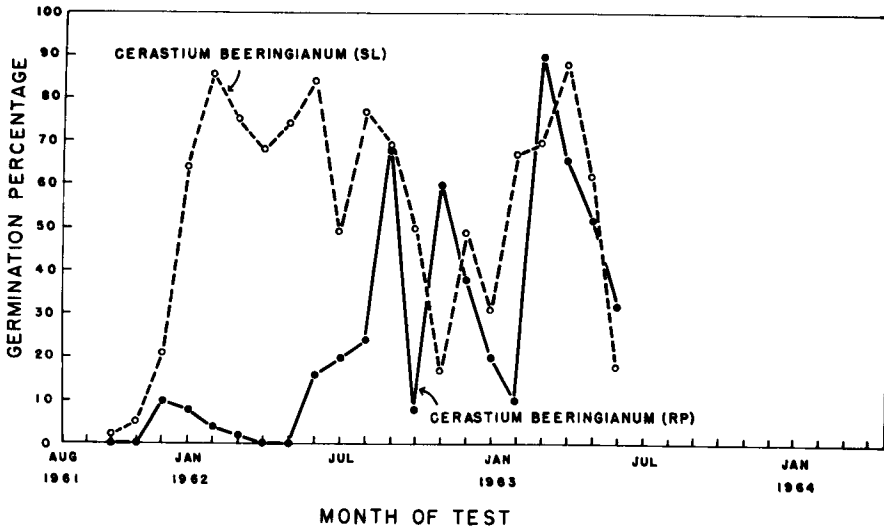


FIGURE 4.

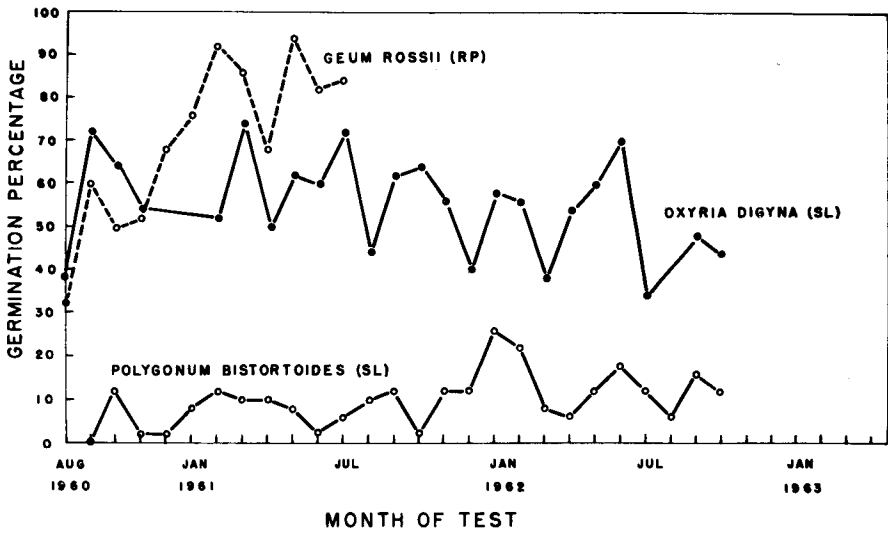


FIGURE 5.

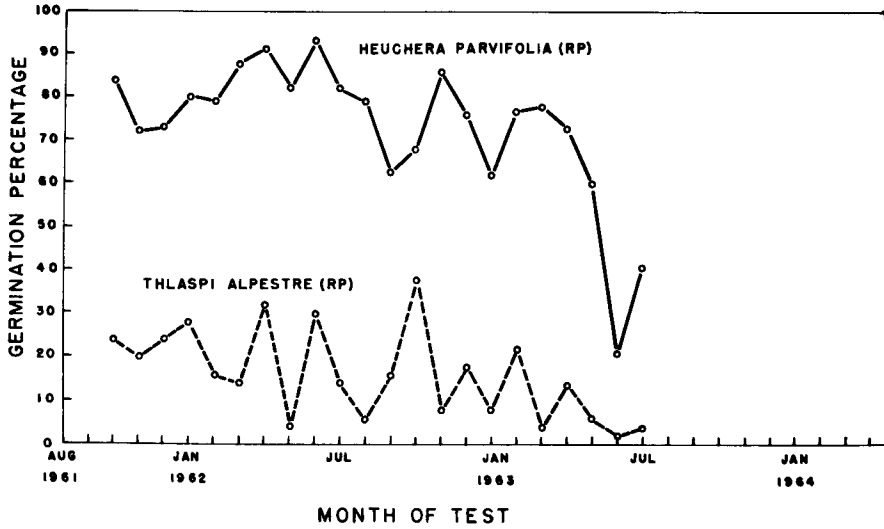


FIGURE 6.

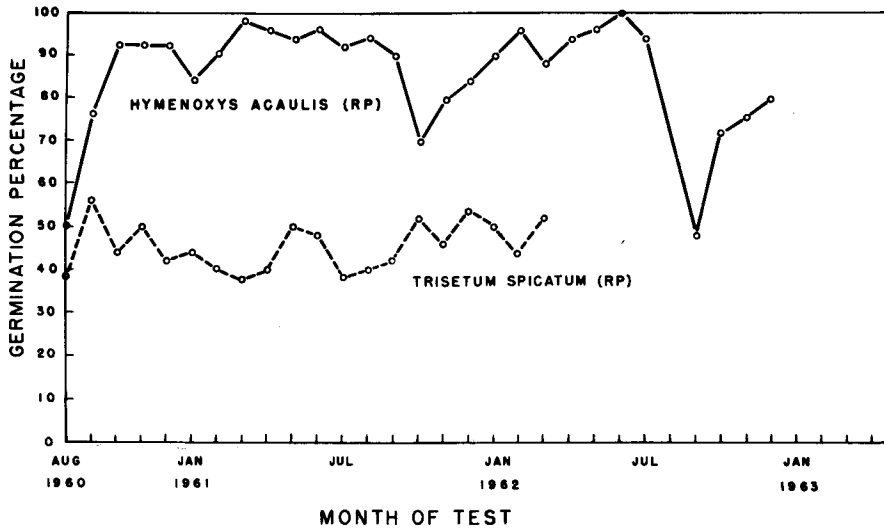


FIGURE 7.

extent between the thirteenth and final fourteenth days of the tests, so the recorded monthly percentages would probably have been slightly higher if the tests had been continued for a longer time.

Hymenoxys acaulis (Pursh) Parker (Figure 7): the seeds were collected August 26, 1960, on Rollins Pass. Freshly-harvested seeds germinated well (50%), and in succeeding months germination was usually almost complete for two years, with some slight decrease in the last four months of the 29-month period of testing. The greatest amount of germination took place in the twenty-second month after harvest.

Hymenoxys grandiflora (Pursh) Parker (Figure 10): the seeds were collected August 26, 1960, on Rollins Pass. Tests were begun the following October and continued for 31 months, with the germination rate remaining more or less constant throughout the entire test period. Bliss found a comparable germination percentage with only a slight beneficial effect of light during germination.

Melandrium furcatum (Raf.) Hulten (Figure 1): the seeds were collected August 18, 1961, on the north side of Summit Lake. Tests were begun in October of 1961 and continued for 22 months. The initial germination rate was very low but rose to nearly 100% in the succeeding months, with occasional unexplained drops, and remained high until the end of the tests.

Oxyria digyna (L.) Hill (Figure 5): the seeds were collected August 19, 1960, on the north side of Summit Lake. Tests were begun with the fresh seeds and continued for 23 months more. Germination was fairly good initially and remained so throughout the test period, with some indication, however, of a gradual decline in germinability. Söyrinki found that seeds of this species from northern Finland germinated 94% with dry cold treatment and 89% without, eight-nine months after collection.

Penstemon whippleanus Gray (Figure 9): the seeds were collected August 25, 1961, near Rollins Pass. No germination took place in the initial test in October, and germination remained below 10% throughout the following 21 months of testing. The apparent dormancy of the seeds of this species was not investigated further.

Phacelia sericea Hook. (Figure 8): the seeds were collected August 5, 1960, and August 25, 1961, near Rollins Pass. Tests on the 1960 seeds were made on the fresh seeds and for the 32 following months. The seeds were initially dormant, but the germination percentage gradually rose during the first year and remained fairly high throughout the remainder of the test period. The tests of the 1961 seeds were performed with 200 seeds each month and showed the same pattern as the 1960 seeds, over a 22-month period.

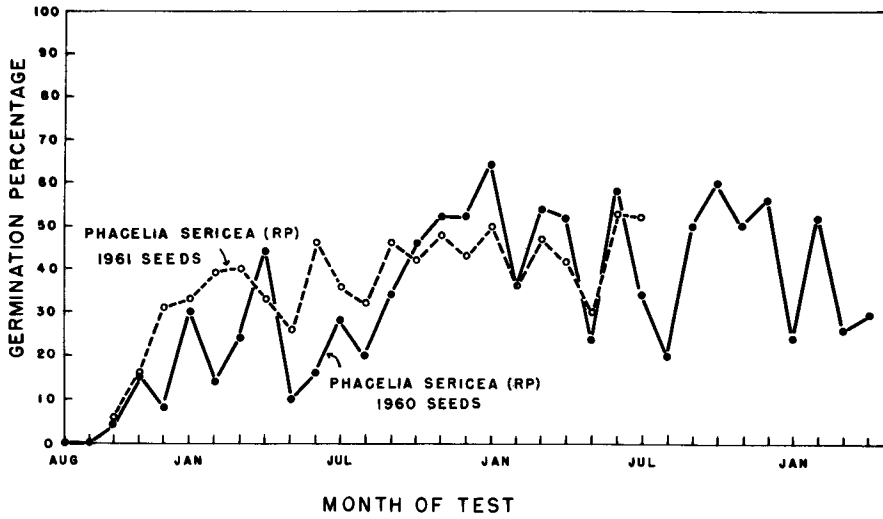


FIGURE 8.

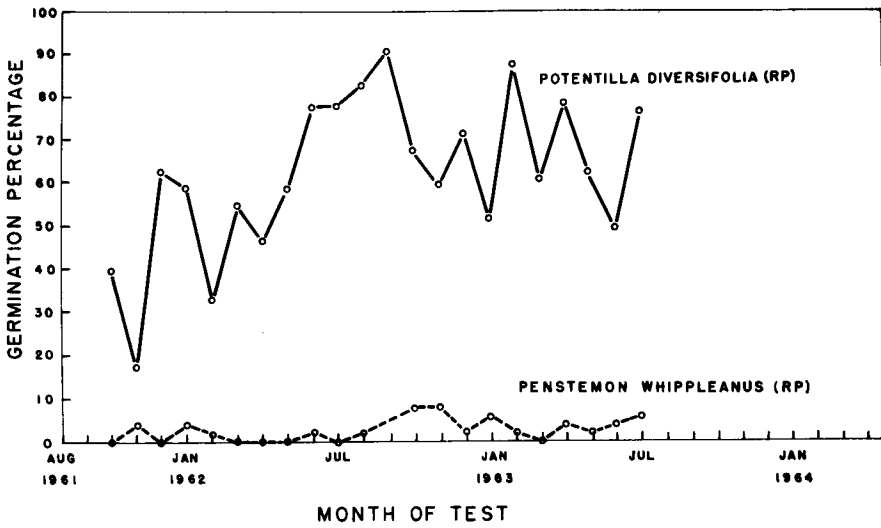


FIGURE 9.

Polygonum bistortoides Pursh (Figure 5): the seeds were collected August 19, 1960, on the east side of Summit Lake. The seeds were completely dormant when tested in September, and germination attained a maximum of only 26% 17 months after harvest. The germination rate remained low but fairly constant throughout the 26-month test period. Bliss reported a reduction in germination in the dark, with the light percentage being comparable to that found here.

Potentilla diversifolia Lehm. (Figure 9) : the seeds were collected September 1, 1961, near Rollins Pass, and tests were begun in October, with 200 seeds being tested each month. The initial germination was fairly low but rose and remained high until the end of the 22-month test period. Bliss found a slight promoting influence of light on the germination of a small seed sample of this species, but the percentage was considerably lower than those found in the present study.

Sibbaldia procumbens L. (Figure 10) : the seeds were collected October 8, 1960, on Rollins Pass. The initial germination of the freshly-collected seeds was quite high and gradually rose and maintained a high rate throughout the 24-month test period. Bliss found only a very slight beneficial effect of light on germination. The percentage of germination of seeds six or seven months old in his study is comparable to that found in the tests reported here. Söyrinki found 100% germination in the sample of cold-treated seeds of this species from northern Finland which germinated best, eight-nine months after collection, and 99% in seeds not given dry cold treatment.

Silene acaulis L. (Figure 11) : the seeds were collected August 5, 1960, and August 25, 1961, on Rollins Pass. The tests were made on the 1960 seeds for 33 months, beginning with the freshly harvested seeds. The initial germination was quite good, and a general trend toward improved germination was noted with time, a maximum of 100% being attained the thirty-second month. Two hundred of the 1961 seeds were tested each month for 20 months beginning in October. The germination pattern is virtually identical to that of the 1960 seeds. Germination continued to some extent during the last days of counting, so the monthly percentages would probably have been higher if the tests had been continued for longer than 14 days. Bliss found that seeds kept in the dark germinated slightly better than those in light. Germination percentages in the present study did not attain the levels found by Bliss for six or seven-month-old seeds until approximately two years after harvest. Söyrinki tested seeds of this species from northern Finland eight-nine months after harvest and reported 99% germination after dry cold treatment and 95% without treatment.

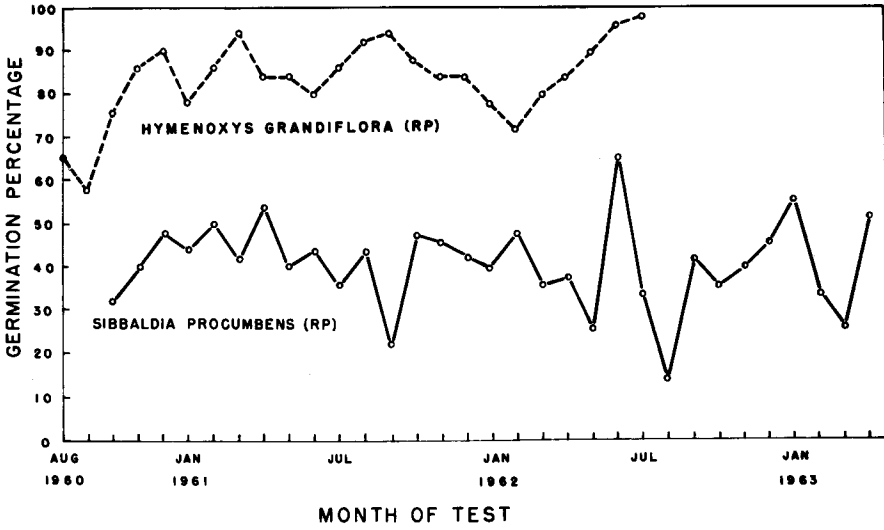


FIGURE 10.

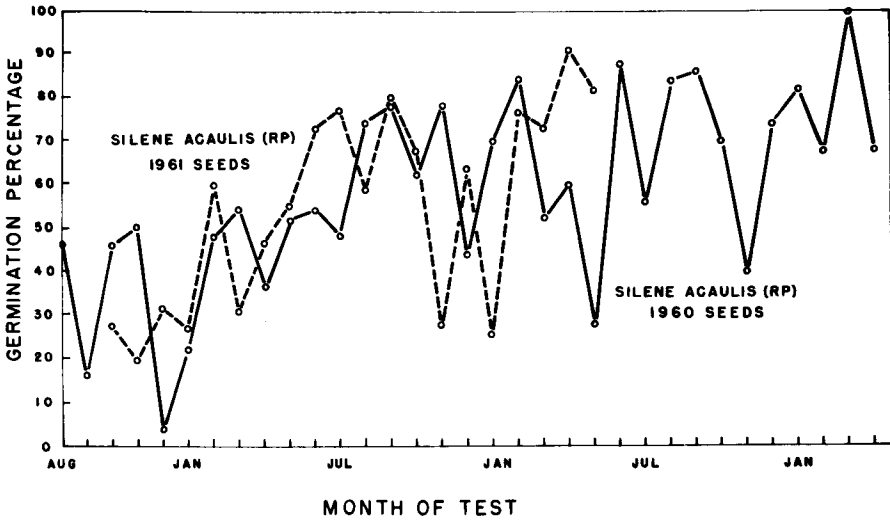


FIGURE 11.

Thlaspi alpestre L. (Figure 6): seeds were collected August 25, 1961, on Rollins Pass. Tests were begun the following October and continued for 21 more months. The initial germination rate was low and gradually decreased to almost nothing at the end of the test period.

Trisetum spicatum L. (Richt.) (Figure 7): the seeds were collected August 26, 1960, on Rollins Pass. Initial germination of fresh seeds was fairly good, and the percentages remained essentially constant throughout the 20 months of testing. Bliss noted an inhibiting effect of light on germination, with results comparable to those reported here.

DISCUSSION AND SUMMARY

Some general observations that may be made from the germination studies are the following:

1. In the 19 species tested, long-continued dormancy appears to be an important factor in relation to germination in only a few (*Penstemon whippleanus*, *Polygonum bistortoides*, *Thlaspi alpestre*), although dormancy as such was not studied. Pronounced dormancy occurred in the fresh seeds of a number of species but was gradually overcome without any special treatment (*Antennaria alpina*, *Arenaria rubella*, *Cerastium beeringianum*, *Melandrium furcatum*, *Phacelia sericea*). Bliss (1958) found that seeds of 21 of 26 alpine species from Wyoming germinated when tested six to seven months after harvest at 72° F., and Nichols (1934) reported that refrigeration increased germination in 14 of 19 alpine species from New Hampshire.
2. Many species, though showing a good deal of variability during the test period, exhibited a general tendency toward improved germinability with time. These species are listed below with the month of maximum germinability after harvest in the time tested:
 - a. *Antennaria alpina* (twenty-third month)
 - b. *Arenaria obtusiloba* (twenty-fourth month)
 - c. *Arenaria rubella* RP (twentieth month)
 - d. *Cerastium beeringianum* SL (twentieth month)
 - e. *Cerastium beeringianum* RP (twentieth month)
 - f. *Geum rossii* (tenth month)
 - g. *Hymenoxys acaulis* (twenty-third month)
 - h. *Hymenoxys grandiflora* (twenty-fourth month)
 - i. *Penstemon whippleanus* (fifteenth month)
 - j. *Phacelia sericea* 1960 (eighteenth month)

- k. *Phacelia sericea* 1961 (twenty-third month)
 - l. *Polygonum bistortoides* (eighteenth month)
 - m. *Potentilla diversifolia* (thirteenth month)
 - n. *Silene acaulis* 1960 (thirty-second month)
 - o. *Silene acaulis* 1961 (twenty-first month)
3. Several species exhibited a more or less constant rate of germination throughout the test period:
- a. *Sibbaldia procumbens*
 - b. *Trisetum spicatum*
 - c. *Arenaria fendleri*
 - d. *Melandrium furcatum*
4. Only a few species gradually declined in germinability toward the end of the test period. These are listed with the month of maximum germinability:
- a. *Arenaria obtusiloba* SL (eleventh month)
 - b. *Heuchera parvifolia* (eleventh month)
 - c. *Oxyria digyna* (seventh month)
 - d. *Thlaspi alpestre* (fifteenth month)
- None of these became completely non-viable during the approximately two years of testing, and no other species showed complete loss of germinability in up to 33 months of testing.
5. There is some suggestion of periodicity in the germination of seeds of certain species. These are listed below with the months following harvest of germination peaks:
- a. *Antennaria alpina* (thirteenth and twenty-third months)
 - b. *Arenaria obtusiloba* SL (eleventh and twenty-first months)
 - c. *Arenaria rubella* SL (eighth and fourteenth months)
 - d. *Cerastium beeringianum* SL (sixth, tenth, twelfth, and twentieth months)
 - e. *Cerastium beeringianum* RP (fifth, fourteenth, sixteenth, and twentieth months)
 - f. *Hymenoxys acaulis* (eighth and twenty-third months)
 - g. *Hymenoxys grandiflora* (fifth, eighth, fourteenth, and twenty-fourth months)
 - h. *Melandrium furcatum* (eighth, eleventh, and seventeenth months)
 - i. *Phacelia sericea* RP 1960 (ninth, eighteenth, twenty-third, and twenty-seventh months)
 - j. *Phacelia sericea* RP 1961 (eighth, eleventh, eighteenth, and twenty-third months)

- k. *Potentilla diversifolia* (fourth, thirteenth, and eighteenth months)
- l. *Sibbaldia procumbens* (seventh, twenty-first, and twenty-eighth months)
- m. *Silene acaulis* RP 1960 (approximately fourth, fifteenth, nineteenth, twenty-fifth, and thirty-second months)
- n. *Silene acaulis* RP 1961 (approximately thirteenth and twenty-first months)

These peaks may not be statistically significant and may in any event possibly relate to seasonal variations in environmental conditions in the laboratory. Use of the larger seed samples and controlled conditions would be necessary to clarify this question. Periodicity in germination of seeds of *Amaranthus retroflexus* under controlled conditions has been observed by Barton (1945), however. Germination in this species was greatest between eight and ten months and between 18 and 20 months after harvest. A consideration of all the germination peaks listed above reveals that concentrations of the peaks occur in the months of March, June, August, September, January, and April, with June being most prominent and March second in that respect. Little can be said, then, concerning seasonal periodicity in these alpine species as a group, though the individual species may respond to environmental changes in different ways.

6. Daily germination records during each 14-day test show that one of the 19 species began germination on the first day after the beginning of the test, seven began on the second day, ten on the third day, and one on the fourth day. In general the earliest day of germination remained constant for a species throughout the test period, although in a few cases an additional day or two was required for initiation of germination as the seeds aged. No drastic reduction in rate became evident in any species.

Pelton (1956) reported that in germination tests of seeds of various species of subalpine plants from Colorado soon after harvesting, seven were found to lack dormancy. These include *Trisetum spicatum*, which was utilized in the present study, and two species of *Antennaria*. Germination in *Trisetum* was almost complete. The other 11 showed various types of dormancy which could be overcome by scarification or stratification in some species.

* * *

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