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A Study of Seed Dormancy in Eighteen Species of High Altitude Colorado Plants

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A STUDY OF SEED DORMANCY IN EIGHTEEN SPECIES OF HIGH ALTITUDE COLORADO PLANTS

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The investigation reported below involves experimental work dealing with the occurrence and type of seed dormancy exhibited by a number of plants collected at high altitudes in Colorado. The objectives of the work include contributing to an understanding of the autecology of the species studied, as well as aiding in an evaluation of the ecological significance of seed dormancy itself. Collections were made during July and August of 1953 at two localities in Colorado: The Rocky Mountain Biological Laboratory north of Gunnison in the Elk Mountains of south-central Colorado (Gunnison County); and near the former University of Colorado Science Lodge, now the Arctic-Alpine Institute, west of Boulder in the Front Range of Colorado (Boulder County). These localities will be referred to below as R.M.B.L. and Alpine Institute, respectively. The altitudes at which collections were made ranged within what is usually considered to be climatically "subalpine" in Colorado, the lowest collection being at 9200 feet and the highest at 10,000 feet elevation.

The writer wishes to acknowledge the important aid rendered throughout the course of this study both in the field and in the laboratory by his wife, Jeanette S. Pelton. Thanks are also due Dr. William A. Weber, of the University of Colorado, for checking the identifications of the species used, with the exception of *Erythronium grandiflorum*, *Hydrophyllum capitatum*, and *Saxifraga rhomboidea*.

METHODS

Seeds were collected by hand from living plants (not from the ground) at one locality for each species. Dry fruits were shaken in paper bags within one to three days after collection to free the ripe seeds, which were then separated from debris by passing through a series of screens. In this way most of the unripe seeds, which usually were still firmly attached to fruit or inflorescence, were excluded from the material tested. The fleshy fruits of *Sambucus* were crushed and the seeds cleaned by washing through screens; separation by flotation in water was not used since empty as well as filled seeds were desired for viability determinations.

All seeds were air dried and stored in paper envelopes following extraction. Storage temperatures varied for about three weeks after collection, averaging 17°C for the first two weeks (reaching a maximum of 25°C and a minimum

of 7°C); then during transportation from Colorado to Indiana temperatures averaged 27°C for 9 days, reaching an extreme high of 35°C. Subsequently all seeds were stored air-dry in paper envelopes in a constant temperature incubator at 18°C until removed for experimental work.

Germination tests, with exceptions specified under the individual species below, were carried out in Petri dish germinators, with five sheets of filter paper below and two above the seeds, except for the very small seeds of *Saxifraga, Epilobium, Antennaria,* and *Androsace* in which the upper covering of filter paper was omitted. In general, germination tests were performed with duplicate samples of approximately 200 seeds each, cleaned so as to eliminate obviously shrunken or empty seeds (the small seeds under magnification). Caryopses of *Trisetum* were cleaned by eliminating empty florets as seen by transmitted light. De-ionized water was added as necessary to keep the filter paper moist, excess water being carefully drained off. Seeds were considered to have germinated and were removed when the radicle had emerged to a distance equal to the average diameter of the seed. In general, tests were carried out in the dark at a constant 18°C, except where otherwise stated below. This temperature seemed to be satisfactory for many of the species studied, although some of them seemed to have lower optimum temperature requirements and would germinate readily at 8°C in the refrigerator. The scope of the study, however, did not include systematic testing for optimum germination temperatures or other requirements such as light. Special treatments and germination conditions were provided only for those species which would not germinate under the conditions specified above, and these are described below under the particular species to which they apply. Experiments were normally continued until germination had ceased or had dropped to a negligible rate, most of the tests being carried out at least for three to four weeks. The majority of the experiments were completed at Butler University during 1953, 1954, and 1955, but preliminary tests were performed at the Rocky Mountain Biological Laboratory immediately after collection of seed.

At the completion of germination experiments cutting tests were made on the ungerminated seeds, so as to be able to calculate the "real germination percent" (percent germination of normal appearing and filled seeds), as well as the "apparent germination percent" (percent germination of total normal-appearing seeds, both filled and empty).

RESULTS

A summary of the results for each species is presented in Table I. Additional data are provided as follows:

Androsace septentrionalis puberulenta Knuth (202[1]): The highly dormant

[1] Numbers in parentheses refer to the author's voucher collection numbers. With certain exceptions, one set of vouchers has been deposited in the University of Utah herbarium, and a duplicate set retained by the author.

TABLE I

Summary of dormancy and germination tests. Additional data given in text under each species.

Species	Dormancy present or absent	Effective teratment where dormaney present	Real germination percentage[1]
Androsaee septentrionalis	present	acid searifieation	96.6±1.1
A. parvifolia	absent	no treatment necessary	100.0
Antennaria rosea	"	"	96.3±0.9
Cirsium americanum	weakly present	undetermined	50.0±8.0
Epilobium halleanum	present	embryo excision	61.2±11.5
Erythronium grandiflorum	"	moist-cold stratification	96.6± .8
Galium bifolim	"	acid scarification	98.9± .8
Hydrophyllum eapitatum	"	undetermined	negligible
H. fendleri	"	searification plus stratification	31.5±3.3
Lomatium dissectum	"	moist-cold stratification	47.9±3.3
Mertensia fusiformis	"	undeterinined	negligible
Polygonum viviparum	absent	no treatment necessary	100.0
Sambucus microbotrys	present	undetermined	negligible
Saxifraga rhomboidea	"	air-dry 18°C storage	24.9±2.2
Senecio mutabilis	absent	no treatment necessary	99.4± .4
Taraxacum offieinale	"	"	100.0
Thlaspi arvense	present	acid searification	95.0± .6
Trisetum spicatum	absent	no treatment necessary	99.8± .2

[1] Maximum germination obtained from any test, expressed as a percentage of filled and normal-appearing seeds, with the standard deviation of the percentage.

seeds of this species were collected from an open rocky slope at 9,800 feet elevation above the R.M.B.L. on July 27, 1953. Up to 11 months cold-moist stratification at 8°C between moist filter paper in Petri dish germinators was ineffective in breaking dormancy. The only treatment used which resulted in essentially complete germination was concentrated sulfuric acid, indicating the probable cause of dormancy to be an impermeable seed coat. Acid treatment was carried out for 20 minutes, at an average temperature of 24°C. Treated seeds were

washed in running water overnight. Both apparent and real germination were 96.6 ± 1.1[1]%, with a period of 7 days required for the peak rate. Controls showed 39.0 ± 3.0% at the time of the treatment (18 months after collection of seeds), although no germination whatever was obtained from freshly harvested seeds.

Antennaria parvifolia Nutt. (104): Collected August 18, 1953 near the R.M.B.L. on rocky soil in nearly full sun at 9,800 feet altitude. This widely ranging species of open habitats exhibited an apparent germination of 64.4 ± 2.4% and a real germination of 100.0% without treatments, requiring 6 days to reach a peak germination.

Antennaria rosea Greene (103): Abundant on an open cut-over knoll in shallow gravelly soil near the Alpine Institute at 9,800 feet elevation. Collected August 17, 1953. Apparent germination without treatment was 94.2 ± 1.2%, and real germination 96.3 ± 0.9%. Fifteen days were necessary for the peak germination rate to be attained. Germination in this species was atypical in that the radicle emerged after the hypocotyl and epicotyl.

Cirsium americanum (Gray) Robbins. (112): Collected from an open dry meadow above the Alpine Institute at 10,000 feet elevation on August 17, 1953. The heads of this species were heavily infested with larvae, and even the remaining achenes exhibited low viability. Apparent germination without treatment was only 5.0 ± 3.4%, and real germination 50.0 ± 8.0%, the peak being reached in 8 days. Insufficient numbers of viable seeds of this species were obtained to investigate the apparent weak dormancy further.

Epilobium halleanum Hausskn. (200): Seeds of this species were collected on August 4, 1953 above the R.M.B.L. at 9,800 feet elevation, along a dry creek bed in part shade of aspens. Very poor germination was obtained under most of the treatments used, although cutting tests indicated a high viability (over 93%). Eleven months of cold-moist (8°C) stratification resulted in 1.4 ± .4% apparent germination and 1.5 ± .5% real germination upon removal to 18°C. Eighteen months air-dry 18°C storage gave 1.5 ± .4% apparent germination in diffuse light, although when freshly collected no results were forthcoming. Hot water treatments, and pot tests in soil left outdoors overwinter or subjected to combinations of greenhouse and refrigerator temperatures were unsuccessful. Scarification and embryo excision tests strongly suggest that a seed-coat imposed dormancy is present, although sulfuric acid treatment proved impractical because of the minute size of the seeds. In one test seed coats were shaved off one edge of fifty seeds with a sharp razor and 26.5 ±

[1] Standard deviation of the percentage, from the formula $\sigma = \sqrt{\frac{p(1-p)}{N}}$, where p is the germination percentage obtained represented as a decimal and N is the number of seeds upon which the percentage is based.

11.5% developed into seedlings. The remainder of the embryos molded, suggesting that perhaps the real germination was much higher. Only 0.6 ± .6% of the control seeds germinated in this test. In anorher rest, the embryos were excised from eighteen seeds, of which 61.2± 11.5% dveloped into seedlings on filter paper in the dark.

Erythronium grandiflorum ssp *chrysandrum* Pursb. Seeds were collected at 9,800 feet from plants along edges of a dry creek bed in partial shade near the R.M.B.L., on August 4, 1953. A moist-cold stratification between moist filter paper in Petri dishes was found to be sufficient to bteak the profound dormancy of the species. During five months storage under these conditions, 96.0 ± .9% apparent germination and 96.6 ± .8% real germination was obtained without transfet to higher temperatures (all germination occurred at 8°C). One bundted days were required to reach the peak germination at this low temperature. Freshly harvested and 18 month old controls gave no results.

Galium bifolium Wats (109): An abundant species in partial shade at 9600 feet elevation above the R.M.B.L., collected July 15, 1953. No germination was obtained without treatments, but eleven months cold-moist (8°C) storage yielded only 1.4 ± .7% apparent and real germination. Concentrated sulfuric acid for 27 minutes at an average temperature of 27°C was highly successful, however, giving 81.0 ± 3.0% apparent germination and 98.9 ± .8% real germination, as tested on January 5, 1955. Most of the germination occurted at 8°C rather than the 18°C normally used in the test, requiring 6 weeks to reach a peak. Two hundred seeds planted on November 30, 1954, in loam soil in pots and sunken in the soil outdoors gave essentially 100% germination by April 14 in Indianapolis. It is probable that in this case the action of fungi on the seed coat over the winter petmitted the seeds to germinate, since the laboratory tests indicated an impermeable seed coat was involved rather than physiological requirement for a cold treatment. No germination was obtained from either freshly harvested or 18 month old seeds in control runs.

Hydrophyllum capitatum Doug. ex Benth. (250): This is a common early flowering plant collected in part shade of aspens above the R.M.B.L. at 9,800 feet. Seeds were obtained on August 4, 1953, and showed a profound dormancy. Although the seeds exhibited a high viability (92%), only relatively small quantities were extracted and so most of the tests of this species were carried out with half the number of seeds used for the other species. Moist-cold stratification for eleven months gave only 2.7 ± 2.1% apparent germination and 2.8 ± 2.2% real germination and none for the controls. No other treatments were successful for the species, including higher germination temperatures, light treatments, soil tests, sulfuric acid treatment, mechanical scarification, hot water, and combinations of scarification and stratification.

Hydrophyllum fendleri (Gray) Heller (101): Locally abundant along a

stream near the Alpine Institute at 9,500 feet altitude, collected on August 18, 1953. During eleven months cold-moist stratification an apparent germination of 8.6 ± 1.2% and a real germination of 10.2 ± 1.4% were obtained. Controls using either freshly harvested or 18 month old seeds gave no results. Single treatments using sulfuric acid, hot water, and scarification were also unsuccessful. Soil tests, however, in which the seeds were in moist loam at greenhouse temperatures for 6½ weeks and then under moist-cold stratification temperatures (8°C) for 5 months yielded 31.5 ± 3.3% apparent germination. In this case apparent germination closely approximates the real germination percent since sample cutting tests of other seeds from the same lot indicated essentially full viability. Much poorer germination (5.5 ± 1.6%) was obtained from soil tests in which the seeds were in the greenhouse for 13 weeks but at stratification temperatures for only three months. Most germination occurred at 18°C (once dormancy had been broken), but some seeds germinated at 8°C.

Lomatium dissectum multifidum (Nutt.) Math. and Const. (110): Material of this species was obtained at 9,600 feet elevation, near the R.M.B.L. on July 27, 1953, where it is locally abundant on dry rocky slopes. During eleven months at 8°C cold-moist stratification an apparent germination of 40.5 ± 3.2% and a real germination of 47.9 ± 3.3% was obtained with the highly dormant mericarps, a peak not being obtained until 11 months. Germination occurred both at 8°C and subsequently when transferred to 18°C. No germination occurred in either fresh or 18 month old control tests. Several other treatments, including mechanical and chemical scarification, hot-water, and pot plantings in soil left outdoors overwinter were also tried. Of these the outdoor pot cultures yielded the only germination, but this was appreciably lower than the Petri-dish tests, reaching a real germination of only 25.0 ± 3.1%. No results were obtained from pot cultures kept for 6 to 13 weeks in the greenhouse followed by 3 to 5 months at 8°C stratification.

Mertensia fusiformis Greene (120). Collected on July 7, 1953 from 9,800 feet elevation above the R.M.B.L. where the species is a frequent early flowering species in open and semiopen fairly dry sites. After eleven months of moist-cold stratification this dormant-seeded species yielded 4.7 ± 1.3% apparent germination and 11.6 ± 2.0% real germination. Nicking of the seed coat, embryo excision, hot water, sulfuric acid treatment or soil tests did not improve germination appreciably, nor did up to eighteen months of dry storage of 18°C.

Polygonum viviparum L. (108): Locally abundant along a stream in moderate shade above the Alpine Institute at 10,000 feet elevation, where it was collected on August 17, 1953. This species bears bulblets as well as seeds in the inflorescence, but insufficient quantities of the bulblets were collected for testing. Apparent germination of seeds without treatment was 84.7 ± 1.5%, and real germination 100.0%, peak germination being reached in 7 days.

Sambucus microbotrys Rydb. (102): Common along streams near the Alpine Institute at 9,500 feet altitude. Collected August 18, 1953, at a stage when most of the fruits were either yellow or red in color. The profound dormancy was not appreciably affected by moist-cold stratification for eleven months (0.5 ± .36% apparent germination and 1.0 ± 5% real germination). Neither were scarification, hot water, soil cultures, or sulfuric acid treatments effective by themselves.

Saxifraga rhomboidea Greene. A locally common species collected on July 22, 1953 above the R.M.B.L. at 9,800 feet elevation on rather dry rocky soil in nearly full sun. Although freshly harvested seeds were highly dormant, this seems to gradually lessen with age, regardless of storage conditions. After 18 months of air-dry storage at 18°C, an apparent germination of 21.2 ± 2.1% and a real germination of 24.9 ± 2.2% was obtained with a peak at 14 days at 18°C in the dark. Somewhat lower percentages were obtained after eleven months of moist-cold stratification. Hot water treatments, mechanical scarification, germination in diffuse light instead of darkness, and pot tests in soil subjected to various combinations of treatment, including outdoors overwinter, were not successful in hastening the breaking of dormancy in these seeds.

Senecio mutabilis Greene (106): Locally frequent on an open rocky slope above the R.M.B.L. at 9,700 feet. Apparent germination without treatment was 85.6 ± 1.7%, and real germination 99.4 ± .4%, with a peak at 6 days.

Taraxacum officinale Web. (111): This cosmopolitan species is very abundant in open dry meadows. Seeds were collected from the grounds of the R.M.B.L. at 9,500 feet on July 11, 1953. Apparent germination was 94.9 ± .9% and real germination 100.0%. Peak germination was reached in 7 days.

Thlaspi arvense L. (201): This widely spread adventive species is only locally abundant in the vicinity where collected, at 9,200 feet altitude a few miles south of the R.M.B.L. on a dry road cut. The very dormant seeds were obtained on July 27, 1953. Treatment of seeds by cold-moist stratification at 8°C for eleven months resulted in only 0.51± .4% apparent and real germination. Eleven minutes of concentrated sulfuric acid at 32°C, however, gave 68.3 ± 1.3% apparent germination, and 95.0 ± .6% real germination, requiring seven days to reach a peak. Control tests immediately after harvest, and also after 18 months air-dry storage gave no germination at all. Seeds planted in soil in pots left outdoors overwinter gave 41.5 ± 3.6% germination, perhaps as a result of the breakdown of the seed coats by fungal action.

Trisetum spicatum Richt. (105): Collected on August 18, 1953 in an open grassy meadow at 2,700 feet elevation, above the Alpine Institute. Apparent germination without treatments, based on caryopses which appeared filled by transmitted light, was 98.7 ± .6%, and real germination 99.8 ± .2%. Appar-

ent germination based upon seemingly sound fruits not selected with the aid of transmitted light, however, was only 52.4 ± 2.5%, since a large proportion of the caryopses were empty. Peak germination was reached in 14 days.

DISCUSSION

The eighteen species here reported upon can be tentatively classified according to the type of dormancy exhibited as follows:

A. Seeds lacking dormancy and germinating readily in a favorable environment: *Antennaria parvifolia, A. rosea, Cirsium americanum* (partially dormant), *Polygonum viviparum, Senecio mutabilis, Taraxacum officinalis,* and *Trisetum spicatum.* As is frequently the case, the composites and the one grass fall into this category.

B. Seeds possessing a dormancy largely satisfied by a scarification treatment, by acid or mechanical means: *Androsace septentrionalis puberulenta, Epilobium halleanum, Galium bifolium,* and *Thlaspi arvense.* It has not yet been determined whether the inhibition, apparently caused by the seed coat, is a result of impermeability to water or gases, to mechincal restriction, to chemical inhibitors, or othet causes.

C. Seeds requiring only prolonged strarification under moist cold conditions to break their dormancy: *Erythronium grandiflorum* ssp *chrysandrum,* and *Lomatium dissectum multifidum* (partially effective). The physiological processes occurring during such a period may vary with the species, and thetefore this type of dormancy can be caused by several mechanisms (Crocker and Barton 1953).

D. Seeds showing other types of dormancy, such as combined seed coat inhibition and dormant embryos, or dormancy mechanism undetermined: *Saxifraga rhomboidea, Hydrophyllum capitatum, H. fendleri, Mertensia fusiformis,* and *Sambucus microbotrys.*

Where dormancy seems to be present it may eventually be shown that the requirements for germination were not satisfied, and therefore the above classification is strictly tentative.

The results for *Thlaspi* are somewhat at variance with those of Bibbey (1948) who concluded that an overwinter stratification was necessary to break dormancy. In the present series of experiments outdoor plantings did yield up to 42 percent germination, although a moist-cold stratification between filter paper was ineffective by itself. Acid scarification yielded up to 95 percent germination, however, without any stratification treatment. It therefore seems likely that outdoor stratification in soil permits fungi to break down the seed coats sufficiently to permit fair germination the following spring.

The type of dormancy shown by *Saxifraga rhomboidea* is puzzling, since a time factor seems to be the limiting feature. What the morphological or physiological processes are that eventually permit germination to occur have not been determined. On the other hand, several species of *Saxifraga* studied by Webb (1950) show no dormancy at all.

In the case of *Sambucus microbotrys* preliminary experiments suggested that acid scarification followed by moist-cold stratification might yield positive results. A combination seed coat and embryo dormancy would be expected if this species follows the pattern of those members of the genus previously tested (U.S. Forest Service, 1948), although treatments similar to those recommended by this publication were not found to be effective with *S. microbotrys*.

Hydrophyllum capitatum shows profound dormancy probably of a complex nature. Very possibly a combined seed coat and embryo dormancy is present, and that seed coat scarification or decay followed by moist-cold stratification is necessary to break the dormancy. Up to 13 weeks in moist loam soil at greenhouse temperatures, however, followed by three months at 8°C, had no effect.

The results suggest that in *H. fendleri* a strong embryo dormancy requiring moist-cold stratification is present but that a lesser seed coat inhibition must first be removed. The period of time in soil at greenhouse temperatures was probably sufficient to remove this seed coat restriction through fungal activity, thus permitting subsequent after-ripening of the embryo under conditions of stratification. In these tests the seeds produced extensive roots but the epicotyl did not emerge before termination of the experiment. There may be, therefore, an epicotyl dormancy in this species, but this possibility was not investigated. Very likely both a seed coat inhibition and an embryo dormancy are present also in *Mertensia fusiformis*, although the solution of the problem requires additional experimental work.

The adaptational significance of seed dormancy as a mechanism causing germination to occur at a time or place favorable to the subsequent survival of the seedlings is reasonably well established for certain well-studied plants. Precisely to what extent, however, the occurrence, depth, and mechanism of dormancy of seeds is related to environmental necessities is uncertain for the vast majority of species. In a study of a very large number of California plants, Mirov (1936) has shown significant correlations between the occurrence and type of seed dormancy with altitudinal zone. It was found that at higher elevations a greater proportion of the plants required cold-moist stratification than at lower elevations, but that at any given altitude dormancy may be either present or absent, and if present of several possible types.

Even in the relatively small sample of species reported in the present paper, however, it is apparent that the same climatic condition does not necessarily result in the development of parallel seed behaviot; several species show no

seed dormancy at all, while of the dormant types several mechanisms insuring delayed germination are involved in the different species. This variability in the occurrence of dormancy in different species even under nearly identical climatic conditions does not nullify the possible adaptive value of seed dormancy. The significance of any plant character or process must be viewed in the context of the entite life cycle. In one species the reproductive habits may be so adjusted that delayed germination owing to dormancy may be disadvantageous, whereas another species in the same habitat may require postponement of germination to a subsequent season for satisfactory survival of seedlings. Nevertheless, it may be expected that a given habitat may evoke the evolution of one type of seed behavior more frequently than the same habitat results in the development of other types, and it is for this reason that correlations such as those obtained by Mirov are so strongly suggestive. We may expect that the ecological and evolutionary significance of seed dormancy will be much better understood as its occurrence and mechanisms gradually become better known.

SUMMARY

A study of the occurrence and type of seed dormancy in eighteen species of plants collected in two high altitude regions of Colorado gave the following results:

Seeds lacking dormancy: (1) *Antennaria parvifolia* Nutt. (2) *Antennaria rosea* Greene (3) *Cirsium americanum* (Gray) Robins. (partially dormant) (4) *Polygonum viviparum* L. (5) *Senecio mutabilis* Greene (6) *Taraxacum officinalis* Web., and (7) *Trisetum spicatum* Richt.

Seeds possessing a dormancy requiring seed coat scarification only (by acid or mechanical treatments): (1) *Androsace septentrionalis puberulenta* Knuth (2) *Epilobium halleanum* Hausskn. (embryo excision most effective) (3) *Galium bifolium* Wats, and (4) *Thlaspi arvense* L.

Seeds requiring moist-cold stratification only: (1) *Erythronium grandiflorum* ssp *chrysandrum* Pursh., and (2) *Lomatium dissectum multifidum* (Nutt.) Math. and Const. (partially effective).

Seeds showing other types of dormancy: (1) *Saxifraga rhomboidea* Greene exhibits a dormancy which gradually lessens with age in dry 18°C storage, but has not been successfully broken by any treatments so far attempted. (2) *Hydrophyllum capitatum* Doug. ex Benth., (3) *Hydrophyllum fendleri* (Gray) Heller, (4) *Mertensia fusiformis* Greene, and (5) *Sambucus microbotrys* Rydb. all seem to have a double dormancy involving both seed coat and embryo or other conditions, but will require further investigation.

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