SEED DORMANCY IN HIGH ELEVATION PLANTS: IMPLICATIONS FOR ECOLOGY AND RESTORATION

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Abstract: Seed germination is a crucial event in the life of every sexually reproduced higher plant. A portion of the seeds of many species are dormant; they do not germinate unless specific environmental signals or events occur. The objective of this research was to determine the extent of seed dormancy in 28 species of grasses and forbs from alpine-subalpine areas of the Olympic Mountains, Clallam Co., Washington. Five species were non-dormant. After-ripening improved germination of eight species, five required cold stratification, scarification benefitted four, and some seeds of 11 species required light. Four others failed to germinate at all under the given treatments. At least one species may have possessed more than one dormancy mechanism. Results from this study support recommendations for shallow or surface sowing of seeds to satisfy light requirements and fall-planting to increase the likelihood of natural scarification and cold stratification. The diversity and extent of dormancy mechanisms encountered here suggests that under harsh and uncertain alpine growing conditions, natural selection may favor seeds with a genetic system for dormancy and delayed germination. After-ripening occurred even while seeds were in cold-dry storage, suggesting that ecological studies should not use cold-stored seeds and assume they will behave as though they are freshly matured. Seed dormancy may control germination timing and rate, which in turn effect plant establishment and competitive ability, and ultimately population, successional, and community patterns of high-elevation vegetation. Successful germination protocols improve propagation success and aid efforts to revegetate disturbed areas in Olympic National Park and other high-elevation areas in the Pacific Northwest.

Key words: Seed germination, dormancy, alpine plants, revegetation, National Park

INTRODUCTION

Dormancy in seeds of alpine plants may be considered an adaptation to a harsh environment, where controlled germination can be crucial to seedling survival (Pelton, 1956; Amen, 1966; Bliss 1971). But the extent of seed dormancy in high-elevation floras has been investigated in only a few cases, mostly in the Rocky Mountains (Amen, 1966). In fact, relative to present-day knowledge of alpine plant ecophysiology and community dynamics, alpine seed germination is poorly understood. The objective of this paper is to describe the extent of seed dormancy in 28 species from single populations in alpine-subalpine areas of the Olympic Mountains, Washington.

Seed dormancy is relevant to theoretical and applied plant ecology. Species diversity and community composition in the Olympic Mountains is influenced by site productivity and substrate microrelief (del Moral, 1983; Loneragan and del Moral, 1984), but the effect of germination strategy on vegetation is unknown. It seems likely that seed dormancy plays a role in alpine plant community composition because germination timing and rate influence seedling survival and com

petitive ability (Harper, 1977). Restoration projects in disturbed alpine and subalpine habitats in Olympic National Park and other high-elevation areas should have criteria to select native species for revegetation and information on how best to propagate them. Unfortunately, germination characteristics of most native species are either unknown or unpublished.

Seed dormancy can be defined as a "state in which seeds are prevented from germinating even under environmental conditions normally favorable to germination" (Copeland and McDonald, 1985). This definition is used here to include seeds in which germination is delayed relative to seeds of the same species under the same conditions. Dormancy results from physiological, morphological, and/or physical characteristics of seeds (Baskin and Baskin, 1988) that prevent germination until certain conditions are met. In the present study, seed dormancy was characterized in terms of germination response to after-ripening, abrasion of the seed coat, cold stratification, and light and darkness.

STUDY SPECIES AND COLLECTION LOCATIONS

Seeds (or single seeded fruits such as caryopses and achenes) from twelve graminoid and sixteen forb species (Table 1) were harvested by hand in August or September of 1987 from single populations at the following locations within Olympic National Park, Clallam Co., Washington: on the south face of Blue Mountain at 1700-1800 m elevation (47°57'17"N, 123°15'30"W); along the trail to the Elwha River from Hurricane Hill at 1460-1500 m (47°59'50"N, 123°32'56"W); and at 1675-1700 m near the First Divide area of Mount Angeles (48°00'00"N, 123°32'35"W).

Seeds were hand-cleaned, sorted, and stored in paper packets at 7 °C. For each species, the percentage of the seed collection represented by filled seeds (containing endosperm or large embryo) was estimated into classes (< 30%, 30–70%, and > 70%) as a measure of the seed collection quality. Only filled seeds were used in germination tests. With the exception of mountain owl-clover (*Orthocarpus imbricatus*), an annual forb, all of the species selected for study were perennials. Nomenclature follows Hitchcock and Cronquist (1976).

METHODS

My strategy was to determine if a large proportion (> 30%) of one month old seeds of each species was dormant (would not germinate in light at 20 °C, conditions suitable for germination of most alpine seeds [Amen, 1966]), and if so, to attempt to increase germination through different treatments. In a few cases, no one month old seeds were tested. Instead, germination of nine month old seed was used as a baseline to determine if seeds were dormant, and the effect of after-ripening was not tested. In general, if germination was high (> 70%) in light at 20 °C, no further treatments were applied.

Germination

Depending on seed availability and treatment, 45–300 seeds were put on moist cellulose pads in 10 cm petri plates, stacked in a 40 x 25 x 15 cm clear plastic box, and placed in a 20 °C constant-temperature germinator equipped with cool-white fluorescent lights on an 8 hour photoperiod. Petri plate locations in the germinator were randomly assigned at the outset of the experiment, and randomly repositioned each time seeds were inspected. Germination was defined as the emergence of the radical or cotyledon from the seed coat or pericarp. Germinated seeds were counted every one to three days over the first few weeks, then every one or two weeks as the experiment progressed. Petri plates were left in the germinator until all seeds had germinated or no new germination occurred for at least four days. The maximum monitoring period was 145 days, but was less than 80 days for most species. Frequently, a few (1–4) seeds were contaminated by fungi; these seeds were removed and the sample size was reduced accordingly in calculations of percentage germination. Where fungal contamination was a persistent problem, the seeds were rinsed in a dilute bleach solution.

Dormancy-breaking treatments

Several treatments to break dormancy were applied: after-ripening in dry paper packets at 7 °C for 9 months; darkness; scarification (abrasion) of the seed coat; and/or moist cold stratification of 10 month old seed for 6, 12, and 18 weeks at 5 °C. Only a subset of treatments was applied to each species (see Table 1).

In most cases seed morphology and behavior suggested an effective treatment to break dormancy. For example, legumes with water-impermeable seed coats were likely to benefit from scarification, and seeds that imbibed water but failed to germinate were candidates for prechilling (cold stratification). In some cases, the number of treatments that could be applied was limited by the number of seeds available. Most, but not all, species were germinated under both light and darkness.

Darkness was applied by wrapping two layers of aluminum foil around the plastic box containing the petri plates. The dark-box was placed for a minimum of 18 weeks on the same shelf in the same germinator as the other seeds. Germination of dark-treated seeds was scored only once or twice using a green safety light. Legume seeds (*Astragalus cottonii, Hedysarum occidentale, Lupinus latifolius* var. *subalpinus*, and *Oxytropis viscida*) were scarified in a sandpaper-lined cylinder with air jets that blew the seeds against the abrasive wall. Alpine willow-herb (*Epilobium alpinum* var. *alpinum*) seeds were scarified by hand with a razor blade incision near their cotyledon end. To stratify mountain hairgrass (*Deschampsia atropurpurea*), tufted hairgrass (*D. cespitosa*), mountain owl-clover (*Orthocarpus imbricatus*), bracted lousewort (*Pedicularis bracteosa* var. *atrosanguinea*), spreading phlox (*Phlox diffusa* var. *longistylis*), and small needlegrass (*Stipa occidentalis* var. *minor*), seeds were placed between two sheets of moist filter paper (Whatman® No. 1) in petri plates, wrapped in aluminum foil, and left in a cold room at 5 °C for 6, 12, and 18 weeks.

RESULTS

Seed quality

The seed crop of most species contained a high proportion of filled seeds. Seed-fill was > 70% in seven grasses, 30-70%

TABLE 1. Collection site, percentage of seeds filled, percentage seed germination (%), days to 50% germination (t50), and number of seeds tested (N) under various treatments. All treatments were conducted at 20 °C constant temperature with 8 hr light, except where noted. Collection sites are coded as BM= Blue Mountain, HH= Hurricane Hill, and MA= Mount Angeles. Days to 50% germination are not shown where no germination occurred, or for the dark treatment because rate was not measured for that treatment.

Species	collection site	seeds filled (%)	1 month after harvest						after-ripened (9 mo. after harvest)								stratified (10 mo. after harvest)								
			no treatment			scarified			light			dark		scarified			6 wks			12 wks			18 wks		
			%	t50	N	%	t50	N	%	t50	N	%	N	%	t50	N	%	t50	N	%	t50	N	%	t50	N
GRAMINOIDS:																									
Bromus sitchensis var. aleutensis	HH	>70	50.9	98	(60)	--	--	--	84.0	30	(75)	86.7	(75)	--	--	--									
Carex phaeocephala	BM	>70	87.7	41	(60)	--	--	--	--	--	(75)	--	(75)	--	--	--									
Danthonia intermedia	BM	>70	1.7	97	(60)	--	--	--	49.4	35	(75)	18.7	(75)	--	--	--									
Deschampsia atropurpurea var. latifolia	HH	30-70	--	--	--	--	--	--	62.2	10	(75)	0.0	(75)	--	--	--	52.0	3	(50)	83.0	3	(50)	93.6	4	(50)
D. cespitosa var. cespitosa	BM	>70	--	--	--	--	--	--	26.7	8	(75)	2.8	(75)	--	--	--	82.0	4	(50)	93.7	3	(50)	66.0	5	(50)
Elymus glaucus var. glaucus	HH	>70	76.9	48	(15)	--	--	--	93.1	7	(75)	82.4	(75)	--	--	--									
Festuca idahoensis var. oregona	BM	30-70	91.4	34	(60)	--	--	--	87.8	7	(75)	88.6	(75)	--	--	--									
Phleum alpinum	HH	>70	100	8	(60)	--	--	--	89.9	9	(75)	95.9	(75)	--	--	--									
Poa incurva	BM	30-70	28.3	44	(60)	--	--	--	80.3	8	(75)	5.7	(75)	--	--	--	90.0	*	(50)	93.9	*	(50)	89.6	*	(50)
Sitanion hystrix var. hystrix	BM	<30	100	48	(60)	--	--	--	--	--	--	--	--	--	--	--									
Stipa occidentalis var. minor	BM	>70	1.7	97	(60)	--	--	--	1.3	20	(75)	0.0	(75)	--	--	--	6.0	14	(50)	18.0	6	(50)	38.0	5	(50)
Trisetum spicatum	HH	30-70	97.6	17	(60)	--	--	--	--	--	--	--	--	--	--	--									
FORBS:																									
Achillea millefolium var. alpicola	BM	>70	75.0	7	(60)	--	--	--	73.2	4	(75)	39.1	(75)	--	--	--									
Anemone occidentalis	MA	>70	51.7	18	(60)	--	--	--	73.3	26	(30)	66.7	(30)	--	--	--									
Aster paucicapitatus	HH	<30	0.0	--	(20)	--	--	--	0.0	--	--	--	--	--	--	--									
Astragalus cottonii	HH	30-70	30.0	73	(60)	100	1	(60)	18.5	7	(300)	20.0	(60)	100	1	(300)									
Epilobium alpinum var. alpinum	BM	>70	0.0	--	(60)	100	11	(60)	0.0	--	--	--	--	--	--	--									
Erigeron compositus var. glabratus	BM	30-70	58.3	11	(60)	--	--	--	89.0	13	(75)	90.7	(75)	--	--	--									
E. subtrinervis var. conspicuus	BM	30-70	85.0	7	(60)	--	--	--	92.0	4	(75)	89.3	(75)	--	--	--									
Erysimum arenicola var. torulosum	HH	>70	35.1	32	(75)	--	--	--	62.7	7	(75)	50.7	(75)	--	--	--									
Geum triflorum var. campanulatum	BM	>70		--		--	--	--	96.0	5	(75)	60.0	(75)	--	--	--									
Hedysarum occidentale	HH	>70		--		--	--	--	88.0	1	(50)	--	(50)	100	1	(50)									
Lupinus latifolius var. subalpinus	BM	>70		--		--	--	--	48.9	22	(45)	48.9	(45)	100	1	(50)									
Orthocarpus imbricatus	MA	>70		--		--	--	--	0.0	--	(75)	0.0	(75)	--	--	--	0.0	--	(50)	0.0	--	(50)	0.0	--	(50)
Oxytropis viscida	HH	>70	16.1	10	(60)	100	1	(60)	9.8	5	(60)	7.1	(60)	91.7	1	(75)									
Pedicularis bracteosa var. atrosanguinea	MA	>70		--		--	--	--	0.0	--	(75)	0.0	(75)	--	--	--	0.0	--	(50)	0.0	--	(50)	0.0	--	(50)
Phlox diffusa var. longistylis	HH	<30		--		--	--	--	10.0	115	(20)	10.0	(20)	--	--	--	16.7	42	(30)	27.6	9	(30)	30.0	5	(30)
Thalictrum occidentale	MA	>70	0.0	--	(60)	--	--	--	0.0	--	(45)	0.0	(45)	--	--	--	0.0	--	(50)	0.0	--	(50)	0.0	--	(50)

-- treatment not applied   * seeds germinated during prechilling

in four, and < 30% in one. Ten forb species had > 70% seed-fill, four had 30–70%, and two had < 30% (Table 1). Percentage germination and days to 50% of maximum germination (a measure of rate independent of the total number of seeds that germinate) differed widely from species to species, and often from treatment to treatment (Table 1).

After-ripening

More than 30% of the seeds were dormant at one month after harvest in six of ten graminoids (*Carex phaeocephala, Elymus glaucus* var. *glaucus, Festuca idahoensis* var. *oregana, Phleum alpinum, Sitanion hystrix* var. *hystrix*, and *Trisetum spicatum*) and in two of ten forbs (*Achillea millefolium* var. *alpicola* and *Erigeron subtrinervis* var. *conspicuus*). Aging tended to release seeds from dormancy. Among species tested at both one and nine months, aging at 7 °C increased total germination in four of seven grasses (*Bromus sitchensis* var. *aleutensis, Danthonia intermedia, Elymus glaucus*, and *Poa incurva*) and four of eight forbs (*Anemone occidentale, Erigeron compositus* var. *glabratus, Erigeron subtrinervis* var. *conspicuus, Erysimum arenicola* var. *torulosum*). Germination rate increased (*i.e.* days to 50% germination decreased) with after-ripening in six of seven grasses (*Bromus sitchensis* var. *aleutensis, Danthonia intermedia, Elymus glaucus* var. *glaucus, Festuca idahoensis* var. *oregana, Poa incurva,* and *Stipa occidentalis* var. *minor*) and five of seven forbs (*Achillea millefolium* var. *alpicola, Astragalus cottonii, Erigeron subtrinervis* var. *conspicuus, Erysimum arenicola* var. *torulosum,* and *Oxytropis viscida*).

Darkness

Compared to seeds after-ripened in light, dark-treated seed often showed reduced germination. Darkness inhibited germination in six of nine grasses (*Danthonia intermedia, Deschampsia atropurpurea* var. *latifolia, D. cespitosa* var. *cespitosa, Elymus glaucus, Poa incurva,* and *Stipa occidentalis* var. *minor*) and six of 13 forbs (*Achillea millefolium* var. *alpicola, Anemone occidentale, Erigeron subtrinervis* var. *conspicuus, Erysimum arenicola* var. *torulosum, Geum triflorum* var. *turbinatum,* and *Oxytropis viscida*). The effect of darkness on germination rate could not be determined in this study because seeds in the dark treatment were inspected only once or twice.

Scarification

All five scarified forbs (*Astragalus cottonii, Epilobium alpinum* var. *alpinum, Hedysarum occidentale, Lupinus latifolius* var. *subalpinus,* and *Oxytropis viscida*) showed increased germination total and rate compared to un-abraded seeds.

Stratification

The grasses that were cold stratified (*Deschampsia atropurpurea* var. *latifolia, D. cespitosa* var. *cespitosa, Poa incurva,* and *Stipa occidentalis* var. *minor*) showed marked improvement in germination total and rate relative to non-chilled species, and total germination increased with the length of the stratification period. Spreading phlox (*Phlox diffusa* var. *longistylis*) was the only forb (of four) whose germination total and rate improved with prechilling. Neither stratification, after-ripening, nor dark treatments released any seeds of mountain owl-clover (*Orthocarpus imbricatus*), bracted lousewort (*Pedicularis bracteosa* var. *atrosanguinea*), or western meadowrue (*Thalictrum occidentale*) from dormancy. The viability of these seeds is unknown, but in preliminary tests two weeks after harvest, nine of 40 *Orthocarpus imbricatus* seeds germinated in darkness at 7 °C, suggesting that seeds were viable but conditions to break dormancy were not provided by any of the treatments.

DISCUSSION

Extent and types of seed dormancy

Dormancy in one form or another was present in a portion of one or nine month old seeds of most of the 28 species studied. After-ripening improved germination in at least eight species, five species required prechilling, scarification benefited four, and 11 were promoted by light. Dormancy in the seeds of some species was expressed as a delay in germination relative to other seeds of the same species. For example, nine months after harvest 10% of the mountain oatgrass (*Danthonia intermedia*) seeds germinated in 20 days, but 137 days were required for total germination to reach 40%. The relatively high frequency of "innate dormancy" (Harper 1977)—relieved by after-ripening in 53% of the species tested here—was not surprising. Bonde (1965) showed that germination improves with seed age in several alpine plants, with the notable exception of spike trisetum (*Trisetum spicatum*), which germinated soon after harvest. In this study, 98% of spike trisetum seeds were germinable one month after collection.

Moist prechilling broke dormancy in seeds of four grasses and one forb, but not three other forbs, a feature common among seeds of alpine plants. For example, cold stratification improves alpine seed germination in three of 18 species tested from the Elk Mountains, Colorado (Pelton, 1956), two species from the Colorado Front Range (Amen and Bonde, 1966; Amen, 1966), and four of eight species from the

Beartooth Plateau, Montana (Chambers, 1987). In this study, germination in *Deschampsia cespitosa* increased after prechilling, but germination is significantly reduced when seeds of this species from Montana are cold stratified at 1–2 ºC for 90 days (Chambers, 1987). The effect of stratification may differ from region to region for widely distributed species. It is noteworthy that *Poa incurva* seeds germinated well *during* stratification at 5 ºC in this study, but Sayers and Ward (1966) found no germination below 10 ºC in six alpine species, and Amen (1966) has suggested this is the rule.

Impermeable seed-coats accounted for dormancy in five species tested (42% of the 12 species dormant at one or nine months after harvest), including four legumes and *Epilobium alpinum* var. *alpinum.* This result is close to the 38% incidence of impermeable seed-coat dormancy observed in 21 dormant alpine plants of the Rocky Mountains (Amen, 1966). Scarification was applied selectively in this study, however, so it is possible that it could benefit the seeds of other species as well. Scarification increased germination rate also. Days to 50% germination in Cotton's milkvetch (*Astragalus cottonii*), broadleaf lupine (*Lupinus latifolius* var. *subalpinus*), and sticky crazyweed (*Oxytropis viscida*) dropped from 5-73 days to one day. Similarly, scarified seeds of *Trifolium nanum*, another legume, germinate in 6-8 hours (Amen, 1966).

Light promoted germination in nearly half (nine) of the twenty-two species tested under both light and darkness. No species were strongly dark-promoted. Rather, germination in three species decreased over 35% in the dark treatment relative to their performance in light. Most species tested from Rocky Mountain National Park, Colorado (Sayers and Ward, 1966) and the Beartooth Plateau, Montana (Chambers *et al.,* 1987) also respond favorably to light.

Populations and even individual seeds may possess more than one dormancy mechanism (Baskin and Baskin, 1985). *Poa incurva*, for example, may have exhibited multiple dormancy in this study, responding favorably both to after-ripening and prechilling. Alternatively, these treatments could have accomplished the same thing, since after-ripening was conducted at nearly the same temperature (7 ºC) as cold scarification (5 ºC). Therefore, only one dormancy mechanism may have been involved (C. Baskin, pers. comm.).

Applicability and limitations

The generality of the results for each species is unknown, because the types of seed dormancy and the percentages of seeds that are dormant in any species may vary from population to population, year to year, and even season to season, just as they do in resident soil seed banks (Baskin and Baskin,

1985). For example, dormancy in seeds of *Carex albonigra* seems to alternate yearly from photosensitivity to a scarification requirement, and the proportion of dormant seeds of *C. ebenea* differs among populations (Amen and Bonde, 1964). Conclusions based on the data presented here are tentative because some treatments were incompletely replicated. Despite their inherent limitations, these results offer an initial estimate of the extent of seed dormancy in the alpine flora of the Olympic Mountains.

Ecological implications

Alpine seed dormancy may have evolved in response to a temporally unpredictable environment. Seed germination in alpine areas can be limited to brief periods in the summer when soil water is available (Bliss, 1971). Even after germination, seedlings of alpine plants are vulnerable to sudden frost or drought (Brink, 1964). Soil moisture and temperature from June through September fluctuate markedly at Blue Mountain in the Olympic Mountains (del Moral, 1983), creating uncertain conditions for seedlings, even in the peak growing season. Seed populations that germinate simultaneously may be subject to greater mortality than populations with dormancy mechanisms that allow germination at several episodes, any one of which might prove "best" (Amen, 1966). Therefore, natural selection in alpine areas may favor seeds with a genetic system for dormancy and delayed germination. These results support the notion that seed populations should be viewed as a collection of individuals with potentially differing degrees and/or types of dormancy.

After-ripening occurred even while seeds were in dry storage at low temperatures (7 ºC). This has been demonstrated also for seeds of tall peppergrass (*Lepidium virginicum*) stored at -18 ºC (Toole *et al.*, 1957) and orchard grass (*Dactylis glomerata*) at -75 ºC (Probert *et al.*, 1985). Seeds of spotted knapweed (*Centaurea maculosa*) stored at -15 ºC for 60 days after-ripen completely (Eddleman and Romo, 1988). Therefore, ecological studies of seed germination should not use cold-stored seeds and treat them as freshly matured.

Implications For Restoration

Some Pacific Northwest and Olympic Mountain alpine plant communities are particularly sensitive to trampling and other disturbances (Bell and Bliss, 1973), and restoration projects are underway in disturbed areas of various western National Parks. Revegetation efforts that require seeds of the species examined in this study for plant propagation are not likely to be limited by seed quality because percentage seed-fill was high in most species. Results from the present study support recommendations (Chambers *et al.,* 1988) for shallow or surface planting of seeds to satisfy light requirements and

fall-sowing to improve the chances for natural stratification and scarification.

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