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Abstract

Seeds from 30 species of grasses and forbs native to Pacific Northwest prairies were tested for physical and physiological dormancy. The physical dormancy was determined by mechanically and chemically scarifying seeds. Physiological dormancy was evaluated with cold stratification before germination. Experiments were analyzed individually with ANOVA analysis, and by seed lots through time using multiple regression. Three of the tested species had too little germination to determine what kind of dormancy was present. Physical dormancy was found in three legumes that required a treatment to break the hard seed coat. These species, *Lotus unifoliolatus*, *Lupinus albicaulis*, and *Trifolium willdenovii* also had increased germination following cold stratification. This can be taken as evidence of physiological dormancy. Physiological and physical dormancy together is considered combinational dormancy. Another eight species had increased germination after cold stratification. This included both species that did not germinate without cold stratification (*Aquilegia formosa, Camassia leichtlinii, C. quamash, Heracleum maximum, Lomatium nudicaule, Perideridia oregona*, and *Sidalcea campestris*), and species with germination proportions that increased following stratification (*Eriophyllum lanatum*, and the legumes). Four annual forbs (*Clarkia purpurea, Collomia grandiflora, Gilia capitata, and Madia gracilis*) had increased germination when seeds were cold stratified, but the response was more consistent with a low temperature requirement for germination than physiological dormancy. The remaining 12 species germinated with no pretreatments. Understanding the germination requirements of these species will aid in their propagation for restoration and the provisioning of ecosystem services and may help explain the ecology of these species on the landscape.

Introduction

The time of year a seed germinates can have a significant effect on seedling growth and survival (Shabba and Qian 2008). Plants may have more time to grow larger and produce more offspring when seeds germinate earlier in the growing season (Verdu and Traveset 2005). However, in a variable environment where early emergence might expose seedlings to harsh conditions, mechanisms that prevent germination can increase the likelihood of long term survival (Pake and Venable 1996). Plants have evolved a number of mechanisms that maximize germination at optimal times. Plants can have particular tolerances for temperature or light that increase the likelihood of germination at the right time (Baskin et al. 1993, Hardegree 2006). Some species have seed dormancy, where even under appropriate conditions a seed will not germinate. There are many manifestations of seed dormancy in the plant kingdom, but botanists have classified them into dormancy types based on the specific mechanisms that prevent germination (Baskin and Baskin 2004). Seeds with underdeveloped embryos that need time to develop before germination are considered to have morphological dormancy (Scholten, et al. 2009). Seeds with impermeable layers that prevent the embryo from imbibing water and commencing germination have physical dormancy (Baskin et al. 2004, Rolston 1978). Other species experience physiological changes that affect the ability of the seed to germinate. These physiological dormancy mechanisms often are cued to environmental conditions that signal the beginning or ending of favorable germination seasons. In fact, periods of cold and warm temperatures can cause seeds to cycle between dormant and non-dormant states depending on the time of year (Baskin et al. 1993, Meyer and Kitchen 1992). Two other classes of dormancy involve combinations of these mechanisms. Morpho-physiological dormancy includes both an underdeveloped embryo and a physiological mechanism; combinational dormancy includes both physical and physiological dormancy.

The particular triggers that cause a seed to change dormancy states can differ between species. In some species, a period of warm temperatures brings seeds out of dormancy and they germinate when cooler temperatures arrive at the beginning of winter (Baskin and Baskin 1991). Other species require a period of

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cooler temperatures before germination in the spring (Baskin et al. 1992). Exposing moist seeds to particular temperature conditions in an effort to affect their dormancy state is called stratification. Cold stratification tests have been used to separate species of annual forbs into ecological guilds. Seeds of winter annuals tend to increase in dormancy (reduced germination) following a cold stratification and summer annual seeds decrease in dormancy (increased germination) following a cold stratification (Milberg and Andersson 1998).

Cold stratification may be an important trigger in the Willamette Valley of western Oregon, where I conducted my study. Western Oregon has a Mediterranean climate with wet mild winters and dry summers. In contrast to the dense conifer forests of much of the rest of the region, the Willamette Valley has extensive grasslands with remnant patches of native prairie in areas that have escaped urban and agricultural development. These prairies are important habitat for unique species of plants and animals (Schultz et al. 2003; Wilson and Kuykendall 1999). There is considerable interest in protecting remaining prairie fragments as well as propagating native species for restoration and other plantings. To do this successfully, it is helpful to know the dormancy types of the species present and what treatments can break that dormancy. Various types of seed dormancy are widely reported among grassland species (Jain 1982, Bell et al. 1993, Forbis 2010). There is not an extensive literature on dormancy characteristics of many native Willamette Valley prairie species. However, many of the same species and congeners also occur in the lowland prairies of western Washington (Dunwiddie et al. 2006), where Drake et al. (1998) found most of the 32 native prairie species they tested exhibited some type of dormancy. Taxonomy can be useful when trying to predict whether there is seed dormancy in other species from the Willamette prairie species pool. Physiological dormancy is widely represented across many families, orders, and classes of plants, whereas physical dormancy is more restricted, with the Fabaceae and Malvaceae being two families found in Northwest prairies with documented physical dormancy (Baskin et al. 2000, Baskin and Baskin 2004).

The objective of my study was to characterize the germination requirements of a broad assortment of species commonly used in Willamette prairie restoration. I used common seed pre-treatment techniques, including cold moist stratification and mechanical or acid scarification, to test for the presence of physiological or physical dormancy.

Methods

Seed Sources

A total of 30 species were included in this study, although not all were used in every experiment (Table 1). Nomenclature follows the USDA PLANTS database (USDA, NRCS 2010). All are commonly found in remnant prairies of the Willamette Valley and are available from commercial sources. *Aquilegia formosa, Camassia leichtlinii, Heracleum maximum,* and *Potentilla gracilis* were collected from plants growing on the valley floor in the Corvallis, Oregon area, while *Camassia quamash* was collected from the Cascade foothills near the South Santiam River. The rest of the seed lots came from commercial seed production fields in the Willamette Valley. The harvest dates were not consistently reported so seed age was calculated for each seed lot starting September 30th of the year the seed was acquired even though the seeds were purchased in December. After purchase the seeds were stored in a cabinet at room temperature.

Germination Procedures

Many species do not germinate well when first collected, but require a dry after-ripening period (Forbis 2010). All the trials occurred following at least three months of storage to ensure at least this minimum period of after-ripening before germination treatments were applied. Germination experiments took place over the next two years, which allowed some seed to age up to 22 months before the last germination test took place.

Six separate experiments were conducted. The first experiment was a screening to test the germination of sixteen species commonly used in native prairie restoration projects. The second and third experiments used scarification techniques to test for physical dormancy. The third through sixth experiments tested whether cold moist stratification could break physiological dormancy.

Seeds were germinated on filter paper in plastic Petri dishes. The dishes were placed in a greenhouse where temperatures remained between 15 °C and 25 °C. Most of the germinations took place under natural light between January and May, but the last stratification treatments germinated in June through September. The forbs in experiment one had 50 seeds in each dish; 25 seeds per dish were used in the other experiments. A large seeded species (*Lupinus albicaulis*) in experiment three was tested with 10 seeds per dish. Experiments consisted of two replicates of each species with one exception – the warm greenhouse treatment in experiment six used only one dish per species. Germinating

TABLE 1. All of the species included in at least one germination experiment.

Scientific name and authority	Common name	Family
Achillea millefolium L.	Yarrow	Asteraceae
Aquilegia formosa Fisch. ex DC.	red columbine	Ranunculaceae
Artemisia douglasiana Besser	Douglas' sagewort	Asteraceae
Camassia leichtlinii (Baker) S. Watson	great camas	Liliaceae
Camassia quamash (Pursh) Greene	common camas	Liliaceae
Clarkia purpurea (W. Curtis) A. Nelson & J.F. Macbr.	purple godetia	Onagraceae
Collinsia grandiflora Lindl.	blue eyed mary	Scrophulariaceae
Collomia grandiflora Douglas ex Lindl.	grand collomia	Polemoniaceae
Danthonia californica Bol.	California oatgrass	Poaceae
Deschampsia cespitosa (L.) P. Beauv.	tufted hairgrass	Poaceae
Elymus glaucus Buckley	blue wildrye	Poaceae
Elymus trachycaulus (Link) Gould ex Shinners	slender wheatgrass	Poaceae
Eriophyllum lanatum (Pursh) Forbes	Oregon sunshine	Asteraceae
Festuca roemeri (Pavlick) Alexeev	Roemer's fescue	Poaceae
Gilia capitata Sims	globe gilia	Polemoniaceae
Heracleum maximum Bartram	cow parsnip	Apiaceae
Hordeum brachyantherum Nevski	meadow barley	Poaceae
Koeleria macrantha (Ledeb.) Schult.	prairie junegrass	Poaceae
Lomatium nudicaule (Pursh) J.M. Coult. & Rose	barestem desert parsley	Apiaceae
Lotus unifoliolatus (Hook.) Benth.	spanish clover	Fabaceae
Lupinus albicaulis Douglas	sickle-keeled lupine	Fabaceae
Madia gracilis (Sm.) D.D. Keck	slender tarweed	Asteraceae
Perideridia oregana (S. Watson) Mathias	Oregon yampah	Apiaceae
Potentilla gracilis Douglas ex Hook.	slender cinquefoil	Rosaceae
Prunella vulgaris L.	self heal	Lamiaceae
Rupertia physodes (Douglas ex Hook.) J. Grimes	scurfpea	Fabaceae
Ranunculus orthorhynchus Hook.	straight-beaked buttercup	Ranunculaceae
Sanguisorba annua (Nutt. ex Hook.) Nutt. Ex Torr. & A. Gray	prairie burnet	Rosaceae
Sidalcea campestris Greene	meadow checkermallow	Malvaceae
Trifolium willdenovii Spreng.	tomcat clover	Fabaceae

seeds in each dish were tallied daily and water was added as necessary. Germination was defined as the emergence of a recognizable radical from the seed coat. Experiments were terminated after at least two days without any new germination in any of the species. The final proportion of seeds germinating was recorded for each dish.

Scarification

Mechanical and chemical scarification tests were performed on species with low germination in experiment one to test for physical dormancy. In experiment two, seeds were rolled between two sheets of sandpaper for two minutes to mechanically scarify the seeds. The sandpaper was checked for dust and the seed coats checked for damage to ensure effective scarification. In experiment three, seeds were scarified with concentrated sulfuric acid. Seeds of each species were placed in acid for 30 minutes, removed, washed with several changes of de-ionized water, and placed in Petri dishes for germination or additional treatments.

Cold Moist Stratification

Seeds undergoing cold stratification were prepared as usual, but Petri dishes were placed on a shelf in a walk-in refrigerator that effectively maintained 5 °C temperature. The dishes were separated into groups to receive the same treatment, and placed in covered boxes. The boxes were occasionally checked to ensure the seeds remained moist, subjecting the seeds to several periods of light; otherwise the seeds were in the dark.

The Experiments

The first experiment screened the species acquired in year one for the potential presence of dormancy. Experiments two, three, and four included species with low germination in experiment one and subjected them to treatments designed to break specific types of dormancy. Experiments five and six also tested for the presence of dormancy, but included additional species acquired in the second year of testing.

Experiment two subjected two sets of seeds of each species to sandpaper scarification. Following the scarification treatment the scarified seeds and two sets of non-scarified seeds of each species were germinated in the greenhouse. Species with increased germination after scarification were classified as having physical dormancy.

Both a scarification treatment and a cold moist stratification treatment were included in experiment three. Four sets of seeds of each species were scarified in sulfuric acid before being placed in Petri dishes; another four sets were placed directly into Petri dishes as controls. Two sets of each treatment were then placed in the greenhouse for germination, and the other two sets were cold stratified for 44 days. The acid scarification and cold stratification treatments tested for physical and physiological dormancy, respectively. Species with germination increases following scarification and cold stratification were categorized as combinational dormancy.

Experiments four and five tested several species to determine the effect of cold moist stratifications (49-190 days) on physiological dormancy (Table 2). Experiment four only included species tested in experiment one while experiment five included additional species and was started at a later date than experiment four.

Experiment six subjected 28 species to 62 day cold moist stratification treatments to test for physiological dormancy. The three sets of stratified seeds of each species and three sets of dry seeds were set out in naturally lit greenhouses set to maintain different temperatures. Two dishes for each treatment were placed in a cooler greenhouse set to maintain 18 °C in the daytime and 13 °C at night. A single dish for each treatment was placed in a warmer greenhouse set to maintain 24 °C daytime temperatures and 18 °C at night. Actual temperatures varied around the settings during sunny or cold weather, but the cool greenhouse had consistently lower temperatures than the warm greenhouse.

Data Analysis

One-way ANOVA was used to test the separate effects of the treatments in each experiment. Experiments three and six included two types of treatments; in these experiments two-factor ANOVA models were used. Experiment three had enough replication to test for both main and interaction effects, but in experiment six there was only enough replication to test for the significance of main effects. Combining all the experiments together allowed for comparisons based on the additional factors of seed age and seed lot. Seed age was measured from September of the harvest year to the day the seeds were placed in the greenhouse for germination. A multiple regression model including continuous stratification duration and seed age terms, and indicator variables for mechanical and acid scarification and seed lot (when applicable), was used to fit the data from experiments one through six for each species.

Results

Experiment 1: Initial Germination Test.

In experiment one, more than 85% of the seeds germinated in four species—*Koeleria macrantha, Prunella vulgaris, Clarkia purpurea*, and *Hordeum brachyantherum*. Four species—*C. quamash*, *Collomia grandiflora*, *Collinsia grandiflora*, and *Lotus unifoliolatus*—had less than 3% germination, and the remainder had moderate germination levels (Table 3). Species with poor

TABLE 2. The treatments applied in each experiment.

Experiment	Stratification duration (days)	Scarification treatment	Temperature differences	Species count
1	0	none	none	16
2	0	mechanical	none	6
3	44	acid	none	5
4	49 , 94	none	none	8
5	61 , 98 , 190	none	none	9
6	62	none	warm / cool	28

TABLE 3a. The proportion of germinating seeds of each species for each treatment. The top two rows are the date when each germination trial started, and trials are sorted with earlier trials further left in the table. The duration of the cold moist stratification treatment (if applied) in days is in the next row. If there was a scarification treatment applied it is listed next, sand denotes mechanical scarification with sandpaper, and acid denotes scarification with concentrated sulphuric acid. In experiment six, seeds were placed in a warmer or cooler greenhouse, that treatment is listed in the next row down. The lower part of the graph lists the proportion of seeds that germinated for each species under each treatment. The top row is the treatment mean and the standard deviation listed in parentheses. Values within the same species with different letters in the third row are significantly different based of Fisher's LSD. The *P*-values below each species name is from one-way ANOVA tests for differences between treatments.

	2007	**2007**	**2008**	**2008**	**2008**	**2008**	**2008**	**2008**	**2008**
Germination start date	1/9	5/25	2/9	2/9	2/9	2/9	6/1	7/8	10/8
Stratification duration (days)	0	0	62	62	0	0	61	98	190
Scarification	no	no	no	no	no	no	no	no	no
Other treatment			cool	warm	cool	warm			
	----------		Mean proportion seeds germinating (standard deviation)					----------	
Clarkia purpurea $P = 0.02$	0.95 (0.07) b		0.8 (0.11) b	0.68 (na) b	0.78 (0.03) b	0.08 (na) a			
Elymus glaucus $P = 0.12$	0.68 (0.1) a		0.96 (0) a	0.92 (na) a	0.78 (0.08) a	0.92 (na) a			
Elymus trachycaulus $P = 0.15$	0.1 (0.14) a		0.66 (0.25) a	0.56 (na) a	0.6 (0) a	0.72 (na) a			
Eriophyllum lanatum $P < 0.001$	0.37 (0.07) bc	0.28 (0.06) b	0.48 (0.06) c	0.44 (na) c	0 (0) a	0 (na) a	0.38 (0.08) bc	0.36 (0) bc	0.66 (0.08) d
Festuca roemeri $P = 0.28$	0.32 (0.11) a		0.12 (0.06) a	0.04 (na) a	0.16 (0.11) a	0.04 (na) a			
Hordeum brachyantherum	0.98 (0.02)								
Koeleria macrantha $P = 0.01$	0.89 (0.02) c		0.08 (0) a	0.16 (na) a	0.44 (0.11) b	0.52 (na) b			
Madia gracilis $P = 0.03$	0.49 (0.24) bc	0.12 (0) ab	0.46 (0.03) bc	0.64 (na) c	0.26 (0.14) abc	0 (na) a			
Prunella vulgaris $P = 0.03$	0.92 (0) b	0.9 (0.03) b	0.86 (0.14) b	0.4 (na) a	1 (0) b	0.84 (na) b			

germination were selected for further experimentation to determine if various treatments could increase the proportion of seeds that germinate.

Experiment 2: Mechanical Scarification

Experiment two included the four species with the least germination in experiment one. In addition, I included *Trifolium willdenovii* (a second legume species) and *Gilia capitata,* a species with a seed coat mucilage similar to the non-germinating *Collomia grandiflora* that is also in the Polemoniaceae. Scarification did not improve germination of *C. quamash* and *Collinsia grandiflora* (Figure 1). *T. willdenovii* was the only species with a statistically significant increase in seed germination proportion following mechanical scarification in a one-way ANOVA model ($F_{1,2} = 85$, $P = 0.01$). *Lotus unifoliolatus* did not germinate when untreated, whereas scarified seeds did so at moderately

TABLE 3b. Mean proportion of seeds that germinated for species only included in 2008 trials.

	2008	**2008**	**2008**	**2008**	**2008**	**2008**	**2008**
Germination start date	2/9	2/9	2/9	2/9	6/1	7/8	10/8
Stratification duration (days)	62	62	0	0	61	98	190
Scarification	no	no	no	no	no	no	no
Other treatment	cool	warm	cool	warm			
	----------		mean proportion seeds germinating (standard deviation)				----------
Achillea millefolium $P = 0.33$	0.24 (0.23) a	0.84 (na) a	0.72 (0.28) a	0.88 (na) a			
Aquilegia formosa $P = 0.34$	0.04 (0.06) a	0 (na) a	0 (0) a	0 (na) a	0 (0) a	0 (0) a	0.06 (0.03) a
Artemisia douglasiana $P = 0.02$	0.94 (0.08) b	0.68 (na) b	0.88 (0) b	0 (na) a			
Camassia leichtlinii $P < 0.001$	1 (0) b	0.92 (na) c	0 (0) a	0 (na) a			
Danthonia californica $P = 0.19$	0.14 (0.14) a	0.4 (na) a	0.02 (0.03) a	0.36 (na) a			
Deschampsia cespitosa $P = 0.46$	0.8 (0.28) a	0.48 (na) a	0.88 (0) a	1 (na) a			
Heracleum maximum $P = 0.14$					0 (0) a	0 (0) a	0.08 (0.06) a
Lomatium nudicaule $P = 0.003$	0.06 (0.03) a	0.04 (na) a	0 (0) a	0 (na)	0 (0) a	0 (0) a	0.8 (0.23) b
Perideridia oregana $P = 0.002$	0.26 (0.2) a	0 (na) a	0 (0) a	na	0 (0) a	0 (0) a	0.78 (0.03) b
Potentilla gracilis			0.72 (0)	0.8 (na)			
Rupertia physodes	0 (0)	0 (na)	0 (0)	0 (na)	0 (0)	0 (0)	0 (0)
Ranunculus orthorhynchus $P = 0.51$	0.02 (0.03) a	0.04 (na) a	0 (0) a	0 (na) a			
Sanguisorba annua $P = 0.38$	0.48 (0.11) a	0.44 (na) a	0.72 (0.17) a	0.76 (na) a			
Sidalcea campestris $P = 0.007$	0.1 (0.03) b	0.08 (na) b	0.04 (0) ab	0 (na) a	0 (0) a	0 (0) a	0.1 (0.03) b

TABLE 3c. Mean proportion of seeds that germinated in each experiment for species included in trials throughout 2007 and 2008. *P* – values are from ANOVA tests for differences between treatments. **Lupinus albicaulis* seeds were tested with three stratification durations between June and October 2008, there was no germination in any treatment and they are listed as one value to save space.

	2007	**2007**	**2007**	**2007**	**2007**	**2007**	**2007**	**2007**	**2007**	**2007**	**2008**	**2008**	**2008**	**2008**	**2008**
Germination start date	1/9	2/20	2/21	4/6	4/6	4/6	4/6	4/10	5/25	5/25	2/9	2/9	2/9	2/9	6/1, 7/8, 10/8
Stratification duration (days)	0	0	0	0	44	0	44	49	94	0	62	62	0	0	61, 98, 190
Scarification	no	no	sand	acid	acid	no	no	no	no	no	no	no	no	no	no
Other treatment											cool	warm	cool	warm	
	----------			mean proportion seeds germinating (standard deviation)							----------				
Camassia quamash	0 (0)	0 (0)	0 (0)	0.1 (0.03)	0.01 (0.03)	0 (0)	0.9 (0.03)	0.8 (0.11)	1 (0)	0 (0)	0.98 (0.03)	0 (na)	0 0	0 (na)	
P <0.001	a	a	a	b	a	a	d	c	e	a	e	a	a	a	
Collinsia grandiflora	0.01 (0.01)	0 (0)	0 (0)	0 (0)	0 (0.03)	0 (0.03)	0 (0)	0.02 (0.03)	0.03 (0.04)	0 (0)	0 (0)	0 (na)	0 (0)	0 (na)	
P = 0.56	a	a	a	a	a	a	a	a	a	a	a	a	a	a	
Collomia grandiflora	0 (0)	0 (0)	0.13 (0.13)					0.74 (0.03)	na	0.06 (0.03)	0.73 (0.02)	na	0.02 (0.03)	0 (na)	
P < 0.001	a	a	a					b		a	b		a	a	
Gilia capitata	0.28 (0.03)	0.42 (0.14)	0.44 (0.02)							0.46 (0.03)	0.3 (0.03)	0.6 (na)	0.3 (0.08)	0.16 (na)	
P = 0.01	ab	bc	bc							b	b	c	b	a	
Lotus unifoliolatus	0.02 (0)	0 (0)	0.28 (0.23)	0.14 (0.03)	0.92 (0)	0 (0)	0.24 (0.05)			0 (0)	0.24 (0.06)	0.24 (na)	0.02 (0.03)	0 (na)	
P < 0.001	a	a	c	b	d	a	c			a	c	c	a	a	
Lupinus albicaulis	0.21 (0.1)			0.22 (0.08)	0.34 (0.08)	0 (0)	0 (0)				0 (0)	0 (na)	0 (0)	0 (na)	0* (0)
P < 0.001	b			bc	c	a	a				a	a	a	a	a
Trifolium willdenovii	0.11 (0.01)	0.08 (0)	0.56 (0.15)	0.94 (0.03)	0 (0)	0.18 (0.14)	0.34 (0.2)			0 (0)	0.06 (0.03)	0 (na)	0.04 (0.06)	0 (na)	
P < 0.001	a	a	c	d	a	ab	bc			a	a	a	a	a	

high levels. However, the values were variable and the difference was only marginally significant ($F_{1,2} = 14$, $P = 0.06$). *Collomia grandiflora* ($F_{1,2} = 4$, $P = 0.18$) and *G. capitata* ($F_{1,2} = 0.7$, $P = 0.48$) were unaffected.

Experiment 3: Factorial Cold Moist Stratification, Acid Scarification

Five species were tested in experiment three for their responses to both cold moist stratification and acid scarification. These included two species with negligible germination in experiments one and two (*C. quamash* and *Collinsia grandiflora*), two species that increased germination in response to scarification in experiment two (*T. willdenovii* and *L. unifoliolatus* – both legumes), and a third legume, *Lupinus albicaulis*. No *Collinsia grandiflora* seeds germinated (Figure 2). Ninety percent of untreated *C. quamash* seeds germinated in the cold room before the end of the 49 day period. Only 2% of acid scarified and cold stratified *C. quamash* seeds germinated. Only one seed not held in the cold room germinated. A two-way ANOVA found a strongly significant effect of cold stratification ($F_{1,4} = 487$, $P < 0.001$), acid scarification ($F_{1,4} = 440$, $P < 0.001$), and the interaction ($F_{1,4} = 696$, $P < 0.001$).

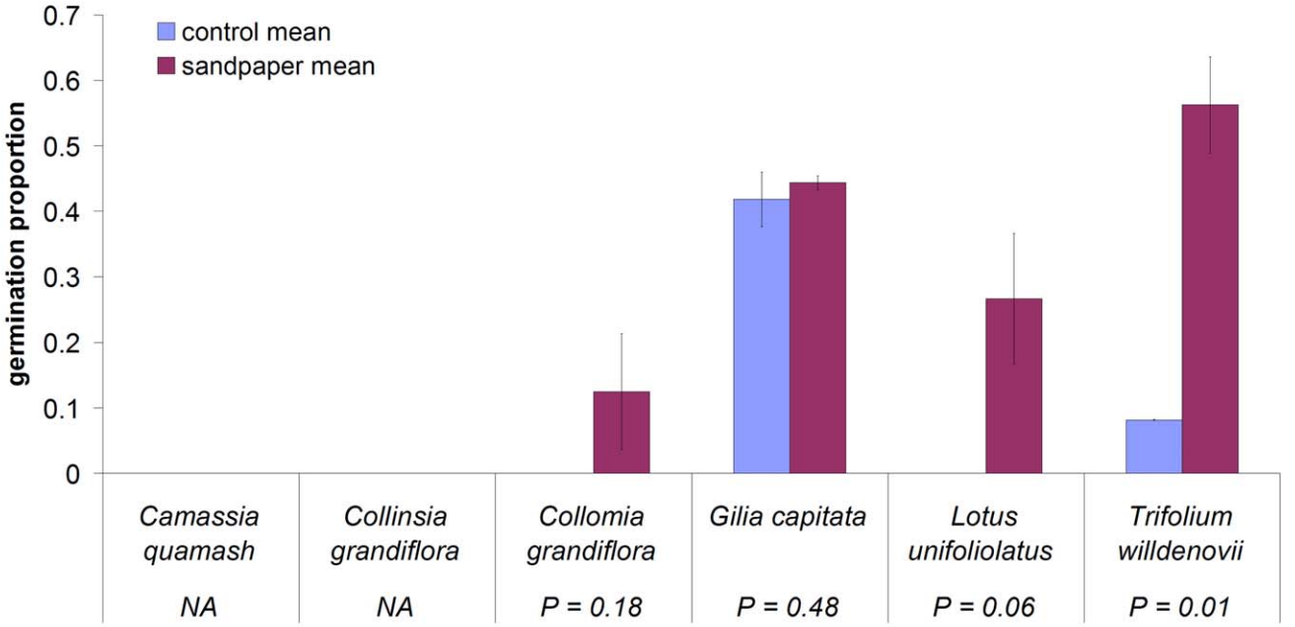

Figure 1. The proportion of seeds germinating in the mechanical scarification experiment. Seeds were either scarified with sandpaper or left as a control before being moistened and placed in the greenhouse. Error bars are standard deviations. P-values are form two sample t-tests.

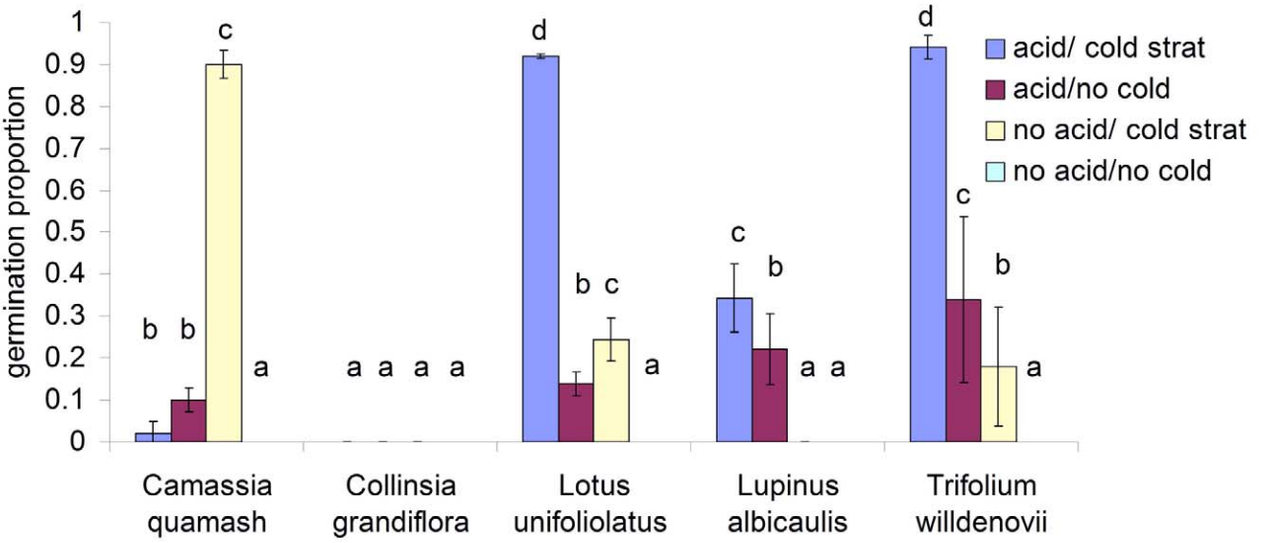

Figure 2. The proportion of germinating seeds of five species after acid scarification with or without cold stratification treatments in experiment three. Error bars are standard error of the mean based on mean squared error of the ANOVA models for each species. Different letters above bars within a species denote significant difference ($P < 0.05$) based on Fisher's LSD.

The three legumes generally responded similarly to one another; untreated seeds did not germinate, and seeds receiving both the scarification and stratification treatments had the highest germination. Seeds of *L. unifoliolatus* germinated more readily when cold stratified than with acid scarification. The two way ANOVA model indicated a highly significant effect of cold stratification ($F_{1,4} = 393$, $P < 0.001$), acid scarification ($F_{1,4} = 618$, $P < 0.001$), and the interaction ($F_{1,4} = 169$, $P < 0.001$). *Lupinus albicaulis* seeds did not germinate without acid scarification leading to a significant effect in the ANOVA model ($F_{1,4} = 46$, $P = 0.002$). Fewer

seeds that only received acid scarification germinated than the seeds with both treatments, but there was not a significant effect of cold stratification ($F_{1,4}$ = 2.1, P = 0.21), or the interaction ($F_{1,4}$ = 2.1, P = 0.21). Germination of *T. willdenovii* increased steadily from cold stratified seeds through acid scarified to doubly treated seeds. The ANOVA model fit a significant effect of stratification ($F_{1,4}$ = 20, P = 0.01), scarification ($F_{1,4}$ = 40, P = 0.003), and suggestive evidence of an interaction ($F_{1,4}$ = 5.9, P = 0.07).

Experiment 4: Cold Moist Stratification 1

Experiment four applied longer cold stratification treatments to the three species with the lowest germination in experiment two. *Collinsia grandiflora* seeds had very little germination and the germination percentage did not significantly differ between treatments ($F_{2,5}$ = 0.7, P = 0.56). *Camassia quamash* seeds did not germinate without stratification, 10% germinated after 44 days of cold treatment, and 80% germinated after removal to the greenhouse (Table 3). All of the *C. quamash* seeds germinated before 94 days in the cold room. Germination percentage significantly differed between treatment groups ($F_{2,5}$ = 266, P < 0.001). All the cold stratified *Collomia grandiflora* dishes had abundant germination at day 38 in the cold room. The germinants were large and starting to die so the dishes were removed. Overall, 70% of the stratified seeds germinated compared to no germination in the control treatment ($F_{1,6}$ = 401, $P = 10^{-6}$).

Experiment 5: Cold Moist Stratification 2

In experiment five, seeds of nine species were cold stratified for two, three, or six months. The trial included species with low germination in previous tests and other species suspected to benefit from cold moist stratification based on taxonomy or personal experience. The seeds of three species, *C. grandiflora*, *L. albicaulis*, and *Rupertia physodes*, did not germinate, regardless of the stratification (Table 3). The percent germination of *Eriophyllum lanatum* almost doubled after the 190 day stratification treatments from the 61 and 98 day level. There was a significant effect of stratification duration on germination percentage in a linear regression model ($F_{1,4}$ = 14.77, P = 0.02). For the rest of the species, no seeds germinated after the two shorter germination periods, but a small percentage of seeds germinated in the longest stratification. There was a significant effect of stratification duration on percent germination of *A. formosa* ($F_{1,4}$ = 15, P = 0.02), *H. maximum* ($F_{1,4}$ = 8, P = 0.05), *Lomatium nudicaule* ($F_{1,4}$ = 25, P = 0.007), *Perideridia oregana* ($F_{1,4}$ = 47, P = 0.002), and *Sidalcea campestris* ($F_{1,4}$ = 27, P = 0.007) seeds in linear regression models.

Experiment 6: Cold Moist Stratification and Germination Temperature

Experiment six included most of the species from experiment one, except for two species for which there was not enough seed, and additional species first acquired in the second year. *Potentilla gracilis* seed was not cold stratified so only dry stored seeds were tested.

Seeds of *Collinsia grandiflora*, *L. albicaulis*, and *R. physodes* did not germinate. The germination percentage of seven of the 28 species was significantly affected by stratification, and there was suggestive evidence of an effect in another three species (Table 4). Germination of *Collomia grandiflora*, *E. lanatum*, *L. nudicaule*, *L. unifoliolatus*, and *S. campestris* was

TABLE 4. *F*-statistics of the effect of cold moist stratification and warmer greenhouse temperatures on each species in experiment six. Asterisks denote significance level (= 0.1 – 0.05, * = 0.05 – 0.01, ** = 0.01 – 0.001, *** < 0.001. Species with the word "zeros" in the stratification column had no germination in the experiment.

Species	Stratification	Temperature
Achillea millefolium	3	3
Aquilegia formosa	1	0
Artemisia douglasiana	2	10 *
Camassia leichtlinii	1998 ***	3
Camassia quamash	4	3
Clarkia purpurea	2	5
Collinsia grandiflora	zeros	
Collomia grandiflora	1249 ***	0
Danthonia californica	2	16 *
Deschampsia cespitosa	2	0
Elymus glaucus	4	1
Elymus trachycaulus	0	0
Eriophyllum lanatum	263 ***	0
Festuca roemeri	0	2
Gilia capitata	1	0
Koeleria macrantha	46 **	2
Lomatium nudicaule	14 *	0
Lotus unifoliolatus	56 **	0
Lupinus albicaulis	zeros	
Madia gracilis	6	0
Perideridia oregano	2	2
Potentilla gracilis	zeros	
Prunella vulgaris	6	9
Rupertia physodes	zeros	
Ranunculus orthorhynchus	3	0
Sanguisorba annua	7	0
Sidalcea campestris	21 *	4
Trifolium willdenovii	0	2

significantly increased following cold stratification, while germination of *K. macrantha* was reduced (Table 4). Stratification resulted in a marginally significant increase in germination of *Madia gracilis* and a decrease in germination of *P. vulgaris* and *Sanguisorba annua*. *Camassia* seeds that were not cold stratified did not germinate. *C. leichtlinii* germinated in both the cooler and warmer greenhouses, resulting in a significant effect of cold stratification (Table 3). Cold stratified *C. quamash* seeds germinated abundantly in the cool greenhouse, but did not germinate in the warmer greenhouse, resulting in no significant effects in the ANOVA model.

There was a significant effect of temperature in two species, and suggestive evidence of an effect in another two (Table 4). Significantly more *Danthonia californica* seeds germinated in the warmer greenhouse. *Artemisia douglasiana* did not germinate in the warmer greenhouse without cold stratification, but there was good germination in both treatments in the cooler greenhouse. Fewer *P. vulgaris* seeds germinated in the warmer greenhouse, although the effect was only suggestive (Table 4). The greatest number of *Clarkia purpurea* seeds germinated in the cooler greenhouse following cold stratification. Germination was reduced in the warmer greenhouse, particularly for non-stratified seeds; this resulted in only a suggestive effect of temperature on germination.

Seed Lot Analysis

Eleven species were included in multiple experiments and were tested for changes in germination or dormancy over time. Germination of five of the species declined with age, while in six it was unaffected (Table 5). Most of these species were involved in several of the experiments where temperature was not a factor so it was not used in the seed lot model. The exception was *C. purpurea* which was in two experiments, one with controlled temperatures. The temperature factor was included in this species' analysis because a significant interaction resulted in otherwise confusing results (Table 5). Only *E. lanatum* had two seed lots with more than one treatment each, and there was a suggestive evidence of a difference in germination between seed lots (Table 5).

Discussion

Fifteen of the thirty tested species showed no evidence of seed dormancy. All of the tested grasses are in this group. Four of the grasses had high germination in every test, but *Festuca roemeri* germination was low overall. These results support those of other studies that found generally no evidence of dormancy in these grass species (Darris 2001, 2007; Flessner and Trindle 2003; Skinner 2004). In my study, cold stratification hindered *Koeleria macrantha* germination, and this agrees with field observations that spring seedings of this species perform better than fall seedings (Gonzalves and Darris 2008). Other studies have reported evidence of dormancy for a few Pacific Northwest grass species. Populations of *F. roemeri* have greater germination after a 14 day cold moist stratification treatment (Darris et al. 2006). Similarly, Darris et al. (2006) also reported that *D. californica* seeds exposed to cold or warm moist stratification treatments have higher germination compared to untreated seeds. Hulling and nicking seeds also increases germination, suggesting that the

TABLE 5. *F*-statistics measuring the effects of multiple factors in linear regression models describing the proportion germination of species included in both early and late experiments. Symbols represent significance of the F test. (< 0.1, * < 0.05, ** < 0.01, *** < 0.001). Column headings are shortened for space, days strat is the duration of cold stratification treatments, acid scar is acid scarification and sand scar is mechanical (sandpaper) scarification. Temperature was only included in the *Clarkia* model because the other species had several tests with uncontrolled temperature, only *Eriophyllum* included seeds from more than one seed lot.

	Seed Age	Days strat	Acid scar	Sand scar	Temp	Days strat X temp	Seed lot	d. f.
C. quamash	1.8	56***	7.5*	0.5				1/23
C. purpurea	21*	11*			36**	18*		1/3
Collinsia	0.5	0.5	0.1	0.1				1/23
E. lanatum	7.1*	15**					5.6.	1/11
G. capitata	0.8	1.5		0.4				1/12
K. macrantha	127***	45**						1/5
L. unifoliolatus	0	36***	22***	8.2*				1/19
L. albicaulis	24***	3.3.	23***					1/18
M. gracilis	1.1	6.2.						1/5
P. vulgaris	0.4	2.4						1/5
T. willdenovii	8*	9.7**	24***	17***				1/15

seed coat is the source of the dormancy (Darris et al. 2010). In my study, *D. californica* did not exhibit any clear evidence of dormancy, although germination was variable. Some populations of *Deschampsia cespitosa* from high elevations display dormancy, but dormancy has not been reported for Willamette Valley populations (Skinner 2006).

In addition to the grasses, several perennial forbs showed no evidence of dormancy. *Achillea millefolium*, *Artemisia douglasiana*, *Prunella vulgaris* and *Sanguisorba annua* germinated strongly without the need for dormancy breaking mechanisms. A few other studies also have documented no seed dormancy for some native prairie forbs. A test of native prairie species from Washington state populations found 17% of *P. vulgaris* seeds germinated without cold stratification, and none germinated following 12 weeks of cold stratification (Drake et al. 1998). *Sanguisorba annua* seeds showed no evidence of dormancy in this study, which is similar to results from three other *Sanguisorba* species from Alaska (Holloway and Matheke 2003). However, in Moscow, Idaho, *S. annua* seeds had progressively better germination following 45 and 90 day cold stratifications (Skinner 2007a). Also, one field study showed better *A. millefolium* germination in fall than spring plantings, suggesting that cold stratification may improve germination in some populations (Skinner 2003).

Among annual forbs, *Gilia capitata* seed germinated well without treatments, but three others—*Clarkia purpurea*, *Collomia grandiflora*, and *Madia gracilis*—had increased germination in cold stratified treatments. *C. purpurea* seed germination was not consistent across the two temperature environments: seeds that were not stratified germinated much better in the cool greenhouse than the warm greenhouse (8% to 78%; Table 3). Seeds that were cold stratified germinated only slightly better in the cool greenhouse than the warm greenhouse (72% and 68%). *Collomia grandiflora* seed has been previously shown to require cold stratification in another Corvallis trial (Bartow 2003a). However, it is not clear whether these results reflect a strict cold stratification requirement, or simply enhanced germination under cooler temperatures. Germination of *Collomia grandiflora* during the stratification treatment in this study, the *Clarkia* results in experiment six, and evidence from trials in Pullman, WA, suggest that these annuals may not require a cold stratification treatment, but rather are adapted to germinate in cooler temperatures than are often provided in germination trials (Skinner 2005). A study that included many of these annual species found they did have better germination at colder temperatures (Russell 2010). Low temperature germination is likely an adaptation to the wet, mild winters and dry summers of the Willamette Valley. If seeds germinate only at the onset of winter rains and not when the soil warms in the spring, either through dormancy mechanisms or reduced germination at higher temperatures, plants are more likely to have adequate moisture to complete their lifecycle.

I interpret the increases in germination of ten species following cold stratification treatments and suggested in another two as evidence of physiological dormancy. Among these ten, the three Apiaceae species (*H. maximum, L. nudicaule,* and *P. oregana)* only germinated after long term cold stratification treatments (98-190 days). Bartow (2010) reported that *P. oregana* required 90 days of cold moist stratification for good germination. *Lomatium nudicaule* was reported to require cold stratification for Willamette Valley seed (Bartow 2003b), but in a study of seed from Washington prairies, there was no germination with 0, 6, and 12 weeks of cold stratification (Drake et al. 1998). The other *Lomatium* species tested in the Washington study, *L. utriculatum* and *L. triternatum,* both responded to cold stratification, but differed in the optimum duration (Drake et al. 1998). Another species, *Lomatium dissectum,* from the Snake River area of eastern Oregon, was shown to require more than 12 weeks at 3.4 °C for maximum germination (Scholten et al. 2009). During the cold stratification the *Lomatium* embryos more than tripled in size indicating *L. dissectum* has morphological dormancy. Baskin and Baskin (2006) reported that *H. maximum* had morphophysiological dormancy and required 112 days of cold moist stratification. This combination of morphological and physiological dormancy is commonly encountered in members of the Apiaceae and may be present in *P. oregana* as well (Baskin and Baskin 1991, Baskin et al. 1992).

Sidalcea campestris and the two species in the Ranunculaceae, *A. formosa* and *Ranunculus orthorhynchus*, also only germinated after long stratification, but the two germinants overall for *R. orthorhynchus* in this study are not enough to draw strong conclusions. Six weeks of cold stratification slightly increased germination of *Ranunculus occidentalis* from Washington State, but 12 weeks of stratification resulted in no germination (Drake et al. 1998). *Aquilegia formosa* is reported to benefit from at least 6 weeks of cold stratification (Trindle and Flessner 2003). Even when cold stratified, there was low germination in this study of *S. campestris* seed. In another study of the same species, Bartow (2007) found that 45 and 90 day cold stratifications of seeds

did not improve germination, while scarification did. Plants in the Malvaceae are reported to have physical dormancy, so it is possible that the response to stratification observed in experiments five and six is due to degradation of the seed coat allowing germination rather than an actual physiological change in the seed (Baskin et al. 2000).

The two *Camassia* species failed to germinate without cold stratification, but had good germination after shorter duration stratifications. *C. quamash* from western Washington also did not germinate without stratification, whereas six and 12 week stratifications resulted in progressively more germination (Drake et al. 1998). Seeds from Pullman, Washington were reported to require cool germination conditions and a 42 to 100 day cold stratification period (Anonymous 2000).

In this study, *Eriophyllum lanatum* seeds germinated well after 60 day cold stratification treatments, while the longest stratification (190 days) had even more germination. *Eriophyllum lanatum* seeds from western Washington had low germination in untreated seeds, maximum germination after 42 days of cold stratification, and reduced germination after 84 days (Drake et al. 1998). Seeds from eastern Washington do not germinate without treatment, 10% of seeds germinate after 45 days of cold stratification, and 75% germinate after 90 days of cold stratification (Skinner 2007b). These varying results suggest that populations of *E. lanatum* differ in the precise length of cold stratification required. Those differences may reflect adaptations to the different climates around the Northwest.

Other than *R. physodes*, which did not germinate in any trial, the species in the Fabaceae (*L. unifoliolatus, L. albicaulis,* and *T. willdenovii)*, all had increased germination following cold moist stratification. *Lupinus albicaulis* had some germination after experiment one, but by experiment two only seeds that were acid scarified germinated (Table 3). *Trifolium willdenovii* also had sharply reduced germination after dry storage. *Lupinus albicaulis* seed from western Washington had low germination in untreated seeds, higher germination after 6 weeks cold stratification, but no germination after 12 weeks of cold stratification (Drake et al. 1998). The germinating legumes also responded positively to scarification treatments. This form of physical dormancy is commonly found in the legume family (Rolston 1978; Baskin et al. 2000).

Fourteen species showed no evidence of dormancy. Cold moist stratification treatments resulted in increased germination in ten species indicating physiological dormancy. Scarification increased germination in three species indicating physical dormancy. Two species had both physical and physiological dormancy, classifying them as having combinational dormancy. Twelve of the 28 species that were subjected to cold stratification treatments in this study, had increased germination following cold stratification. This compares with 22 out of 30 species from lowland Washington prairies that responded to cold stratification (Drake et al. 1998). The difference could be because in the Washington study there were only two grass species whereas I included seven grasses, none of which responded to cold stratification. The sizes of the embryos were not measured so I can provide no information on whether morphological or morphophysiological dormancy is present in any of these species. Three of the tested species had very low germination regardless of treatment. Either the seeds had low viability or these species may need different dormancy breaking treatments or different germination conditions than were provided in these experiments. Most of the results reported here were supported by evidence found by other researchers, but dormancy can vary within a species. Plants adapted to different elevations or latitudes may differ in their dormancy states (Cavieres and Arroyo 2000). Even plants from the same population can differ in dormancy conditions when availability of resources vary due to competition or differences in the weather (Platenkamp and Shaw 1993, Swain et al. 2006)

The variability in germination responses observed in this study suggests that information about seed germination requirements could be useful in the effective design of seed mixes for restoration plantings. For instance, it may be desirable to use mixes that include a range of germination strategies, particularly in cases when only a single seeding of a restoration site is planned.

Literature Cited

Anonymous. 2000. Propagation protocol for production of Camassia quamash plants; USDA NRCS - Pullman Plant Materials Center, Pullman, Washington. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Bartow, A. L. 2002. Propagation protocol for production of container Perideridia oregana plants. USDA NRCS - Corvallis Plant Materials Center, Corvallis. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Bartow, A. L. 2003a. Propagation protocol for production of container Lomatium nudicaule Pursh plants. USDA NRCS - Corvallis Plant Materials Center, Corvallis. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Bartow, A. L. 2003b. Propagation protocol for production of container Collomia grandiflora Lindley Ann plants. USDA NRCS - Corvallis Plant Materials Center, Corvallis. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Bartow, A. L. 2007. Propagation protocol for production of container *Sidalcea campestris* Greene plants. USDA NRCS - Corvallis Plant Materials Center, Corvallis. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Baskin, J. M., and C. C. Baskin. 1991. Nondeep complex morphophysiological dormancy in seeds of *Osmorhiza claytonia* (Apiaceae). American Journal of Botany 78:588-593.

Baskin, J. M., and C. C. Baskin. 2004. A classification system for seed dormancy. Seed Science Research 14:1-16.

Baskin, C. C., and J. M. Baskin. 2006. Propagation protocol for production of container *Heracleum maximum* Bartr. plants; University of Kentucky, Lexington, Kentucky. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Baskin, C. C., E. W. Chester, and J. M. Baskin 1992. Deep complex morphophysiological dormancy in seeds of *Thaspium pinnatifidum* (Apiaceae). International Journal of Plant Science 153:565-571.

Baskin, C. C., P. L. Chesson, and J. M. Baskin. 1993. Annual seed dormancy cycles in two desert winter annuals. Journal of Ecology 81:551–556.

Baskin, J. M., C. C. Baskin, and X. Li. 2000. Taxonomy, anatomy and evolution of physical dormancy in seeds. Plant Species Biology 15:139-152.

Bell, D. T., J. A. Plummer, and S. K. Taylor. 1993. Seed Germination Ecology in southwestern Western Australia. The Botanical Review 59:24-73.

Cavieres, L. A., and M. T. K. Arroyo. 2000. Seed germination response to cold stratification period and thermal regime in *Phacelia secunda* (Hydrophyllaceae). Plant Ecology 149:1-8.

Darris, D.C. 2001. Arlington and Elkton Blue Wildrye. (ID# 587). USDA-NRCS Corvallis Plant Materials Center, Corvallis, OR

Darris, D.C. 2007. Plant Fact Sheet: Jackson-Frazier Germplasm meadow barley. (ID# 7373). USDA NRCS Corvallis Plant Materials Center, Corvallis, OR.

Darris, D., S. Johnson, A. Bartow. 2006. Plant Fact Sheet: Roemer's fescue. (ID# 6824). USDA NRCS Plant Materials Center, Corvallis, OR.

Darris, D., A. Bartow, and J. Williams. 2010. The effect of scarification and stratification treatments on the germination of *Danthonia californica* from three populations. *In* Darris, D., A. Bartow, and J. Williams (editors), Corvallis Plant Materials Center Technical Report 2010 (ID# 9958), USDA Natural Resources Conservation Service, Corvallis, OR. Pp. 13-18.

Drake, D., K. Ewing, and P. Dunn. 1998. Techniques to promote germination of seeds from Puget Sound prairies. Restoration and Management Notes 16:33–40.

Dunwiddie, P., E. Alverson, A. Stanley, R. Gilbert, S. Pearson, D. Hays, J. Arnett, E. Delvin, D. Grosboll, and C. Marschner. 2006. The vascular plant flora of the south Puget Sound prairies. Washington, USA. Davidsonia 17:51-69.

Flessner, T. R., J. D. C. Trindle. 2003. Propagation protocol for production of *Elymus glaucus* Buckl. Seeds. USDA NRCS - Corvallis Plant Materials Center, Corvallis, Oregon. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Forbis, T. A. 2010. Germination phenology of some Great Basin native forb species. Plant Species Biology 25:221-230.

Gonzalves, P., and D. Darris. 2008. Plant Fact Sheet: Prairie Junegrass. (ID# 8198). USDA NRCS Corvallis Plant Materials Center, Corvallis, OR.

Hardegree, S. P. 2006. Predicting germination response to temperature. I. Cardinal temperature models and subpopulation-specific regression. Annals of Botany 97:1115–1125.

Holloway, P. S., and G. E. M. Matheke. 2003. Seed germination of Burnet, *Sanguisorba* spp. Native Plants Journal 4:95-99.

Jain, S. K. 1982. Variation and adaptive role of seed dormancy in some annual grassland species. Botanical Gazette 143:101-106.

Meyer, S. E., and S. G. Kitchen. 1992. Cyclic seed dormancy in the short-lived perennial *Penstemon palmeri*. Journal of Ecology 80:115-122.

Milberg, P., and L. Andersson. 1998. Does cold stratification level out differences in seed germinability between populations? Plant Ecology 134:225-234.

Pake, C. E., and D. L. Venable. 1996. Seed banks in desert annuals: Implications for persistence and coexistence in variable environments. Ecology 77:1427-1435.

Platenkamp, G. A. J., and R. G. Shaw. 1993. Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. Evolution 47:540-555.

Rolston, M. P. 1978. Water impermeable seed dormancy. The Botanical Review 44:365-396.

Russell, M. C. 2010. Germination and establishment in Willamette Valley native prairie plants. M.S. Thesis, Oregon State University, Corvallis.

Scholten, M., J. Donahue, N. L. Shaw, and M. D. Serpe. 2009. Environmental regulation of dormancy loss in seeds of *Lomatium dissectum* (Apiaceae). Annals of Botany 103:1091-1101.

Schultz, C. B., P. C. Hammond, and M. V. Wilson. 2003. The biology of Fender's blue butterfly (*Icaricia icarioides fenderi*) an endangered species of western Oregon native prairies. Natural Areas Journal 23:61-71

Shahba, M. A., and Y. L. Qian. 2008. Effect of seeding date, seeding rate, and seed treatments on Saltgrass seed germination and establishment. Crop Science 48:2453-2458.

Skinner, D. M. 2003. Propagation protocol for production of container *Achillea millefolium* L. plants. USDA NRCS - Pullman Plant Materials Center, Pullman, Washington. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Skinner, D. M. 2004. Propagation protocol for production of container *Elymus trachycaulus* (Link) Gould ex Shinners plants. USDA NRCS - Pullman Plant Materials Center, Pullman, Washington. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).

Skinner, D. M. 2005. Propagation protocol for production of container *Collomia grandiflora* Dougl. ex Lindl plants. USDA NRCS - Pullman Plant Materials Center, Pullman, Wash-

ington. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).
Skinner, D. M. 2006. Propagation protocol for production of container *Deschampsia caespitosa* (L.) Beauv. plants (10 cu. in.). USDA NRCS - Pullman Plant Materials Center, Pullman, Washington. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).
Skinner, D. M. 2007a. Propagation protocol for production of container *Sanguisorba occidentalis* Nutt. plants (10 cu. in.). USDA NRCS - Pullman Plant Materials Center, Pullman, Washington. Available online at http://www.nativeplantnetwork.org (accessed 10 November 2010).
Skinner, D. M. 2007b. Propagation protocol for production of container *Eriophyllum lanatum* (Pursh) Forbes plants (10 cu. in.). USDA NRCS - Pullman Plant Materials Center, Pullman, Washington. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).
Swain, A. J., Z. S. Hughes, S. K. Cook, and S. R. Moss. 2006. Quantifying the dormancy of *Alopecurus myosuroides* seeds produced by plants exposed to different soils moisture and temperature regimes. Weed Science 46:470-479.

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Trindle, J. D. C., and T. R. Flessner. 2003. Propagation protocol for production of container *Aquilegia formosa* Fisch. ex DC. plants (1-yr plugs (10). USDA NRCS - Corvallis Plant Materials Center, Corvallis, Oregon. Available online at http://www.nativeplantnetwork.org (accessed 8 November 2010).
USDA, NRCS. 2010. The PLANTS Database. National Plant Data Center, Baton Rouge, LA 70874-4490 USA. Available online at http://plants.usda.gov/ (accessed 13 December 2010).
Verdu, M., and A. Traveset. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. Ecology 86:1385-1394.
Wilson, M. V., and K. Kuykendall. 1999. Threatened and endangered plants: Incorporation of sensitive species into the database and predictive model of New Strategies for Prairie Conservation, Restoration, and Management. Report to the Bureau of Land Management. Available online at http://people.oregonstate.edu/~wilsomar/PDF/WK_BLM_99.pdf (accessed 20 December 2010).