REFEREED RESEARCH ARTICLE

Chilling requirements for seed germination
of 10 Utah species of perennial

Wild Buckwheat

(*Eriogonum* Michx. [Polygonaceae])

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Figure 1 • *Cushion buckwheat* (Eriogonum ovalifolium) *flowering in the wild at Butler Wash, Utah.*

Wild buckwheats (*Eriogonum* Michx. [Polygonaceae]) are useful in the reclamation of disturbed land, are important honey plants, and have great potential as drought-tolerant ornamentals (Kay and others 1977; Tiedemann and Driver 1983; Zamora 1994). Most of the approximately 200 species in the genus are found in western North America (Welsh and others 1993).

The interesting habits and attractive flowers of wild buckwheat species make them logical candidates for home xeriscapes, but as yet these species are not in the commercial nursery trade (Figures 1 to 3). To date we know of only 2 named germplasm releases, *E. umbellatum* 'Sierra' (Stevens and others 1996) and *E. niveum* 'Umatilla' (Tiedemann and others 1997).

There is little published information on the seed germination requirements of wild buckwheats (Kay and others 1977; Belcher 1985; Young 1989; Meyer forthcoming). In this paper, we present results of chilling experiments with the achenes (1-seeded fruits that may be loosely referred to as seeds) of 10 perennial Utah species. Most of these species are of wide occurrence in the Intermountain West and are found in a variety of habitats (Table 1). We have included multiple collections of widely distributed species in order to account for among-population variation in germination requirements.

Abstract

Ten Utah species of perennial wild buckwheat (*Eriogonum* spp.) produced seeds (achenes) that were either nondormant or that lost dormancy during moist chilling. While there were species-specific patterns, seeds collected from low elevations generally had shorter chilling requirements (0 to 8 wk) and faster germination rates in chilling (<11 wk to 50%) than those from high elevations (12 to 24 wk and >15 wk to 50%). The absence of a fraction not responsive to chilling suggests that these species may not form persistent seed banks. Wild buckwheats establish readily from late fall seedings and are also easily greenhouse-propagated from seeds. They deserve wider use as drought-tolerant ornamentals.

KEYWORDS: dormancy, perennial, propagation, stratification, sulfurflower

NOMENCLATURE: Welsh and others (1993)

We discovered in work with several widely distributed Intermountain West genera that seed germination requirements are related to both life history characteristics and habitat (Meyer and others 1989, 1995; Meyer and Monsen 1991; Meyer and Kitchen 1994a). Patterns of dormancy loss and germination in response to environmental variables are often closely tied to features of the habitat, particularly climate (Meyer and others 1989; Meyer and Monsen 1991). In addition to describing germination

TABLE 1

Ecological and horticultural information for Utah Eriogonum species

Species	Common name	Flower color	Flowering season	Habit	Habitat [a]	Distribution
E. alatum Torr. in Sitgr.	wing buckwheat	reddish-yellow	late summer	monocarpic perennial	FW, MB	Southern Rocky Mountains
E. bicolor Jones	pretty buckwheat	pink and white	late spring early summer	cushion plant	SDS, on clay badlands	endemic to central Utah
E. brevicaule Nutt.	shortstem buckwheat	yellow or white	mid to late summer	subshrub	SS, FW, MB	Middle Rocky Mountains
E. corymbosum Benth.	lacy buckwheat	white, pink, or yellow	late summer to fall	shrub	SDS	Colorado Plateau: Uinta Basin
E. heracleoides Nutt.	Hercules or wyeth buckwheat	cream	early to mid summer	subshrub	SS, FW, MB, AS, CF, MM	Northern Rocky Mountains
E. jamesii Benth. in DC.	James buckwheat	yellow	late spring early summer	subshrub	SDS, SS, FW, MB	Southern Rocky Mountains
E. ovalifolium Nutt.	cushion buckwheat	white, pink, or yellow	early to mid spring	cushion plant	SDS, FW, MB	widespread in the West
E. racemosum Nutt	pink smoke	pink	mid to late summer	perennial herb	SS, FW, MB, AS	Southern Rocky Mountains
E. shockleyi Wats.	Shockley buckwheat	white, pink, or yellow	early to mid spring	mat forming	SDS	Southern Rocky Mountains, southwestern US
E. umbellatum Torr. (type ssp.)	sulfurflower buckwheat	yellow	early to mid summer	subshrub	SS, FW, MB, AS, CF, MM	widespread in the West
E. umbellatum ssp. *majus* Hook.	cream sulfurflower buckwheat	cream	early to mid summer	subshrub	SS, FW, MB, AS, CF, MM	widespread in the West
E. umbellatum ssp. *porteri* (Small) Stokes	alpine sulfurflower buckwheat	yellow	late summer	mat forming	CF, MM, AM	Great Basin, Middle Rocky Mountains

[a] SDS=salt desert shrubland; SS=sagebrush steppe; FW=pinyon-juniper woodland; MB=mountain brush; AS= aspen forest; CF=coniferous forest, MM=mountain meadow; AM=alpine meadow.

patterns in response to chilling for 10 wild buckwheat species, we use our data to test a germination model based on environmental variables that we have developed for other genera. More specifically, we use collection site elevation as a rough indicator of severity of winter climate. We test whether collection site elevation is a good predictor of either chilling requirement or mean germination time in continuous chilling. This model may be useful for predicting the chilling requirements of wild buckwheat seedlots of unknown dormancy status.

Materials and Methods

We made 24 achene collections for this study in summer 1997 (Table 2). For each collection, dried perianths with enclosed achenes were hand-stripped from at least 20 plants. For all species except *E. alatum*, the thoroughly dried material was hand-rubbed through a 2-mm round-hole screen to free achenes from perianths. Achenes were then separated from the floral debris using a tabletop model blower. The large achenes of *E. alatum* were essentially free of the tiny perianths after harvest and did not require additional cleaning.

The above rubbing and blowing procedure worked well for all other species except *E. shockleyi* and *E. bicolor*. Achenes of these 2 species were held tightly in a hardened basal perianth cup and could not be rubbed free without damage. Thus, individual achenes were removed by dissection under a binocular microscope. Because of very low fruit set, collections of these species could be used in only a subset of the treatments.

We determined mean mass of air-dry achenes by weighing a 100-achene sample and dividing the mass by

100. Achene collections were stored under laboratory conditions (20 to 22 °C (68 to 72 °F), 30% to 40% relative humidity) in paper envelopes until initiation of experiments in October 1997.

We included 6 treatments in the chilling experiment: 0, 2, 4, 8, 12, 16, and 24 wk of moist chilling at 2 °C (36 °F) in the dark. Following chilling treatments, achenes were incubated 4 wk under a daily alternating temperature and photoperiod regime (12 h dark at 10 °C [50 °F] and 12 h light at 20 °C [68 °F]) with cool white fluorescent light.

TABLE 2

Collection location and date, and mean achene mass (based on mass of 100 achenes) for Utah collections of Eriogonum

Collection	Location	County	Elevation (m [a])	Date (1997)	Achene mass (mg [b])
E. alatum 1	East of Soldier Summit	Utah	2210	8 Aug	5.5
E. alatum 2	South of Escalante	Garfield	2060	27 Aug	6.0
E. alatum 3	South of Torrey	Wayne	2250	27 Aug	6.1
E. bicolor	Notom Cutoff	Wayne	1450	21 Jul	1.0
E. brevicaule 1	West of Soldier Summit	Utah	1880	8 Aug	1.6
E. brevicaule 2	Scipio Cutoff	Millard	1790	26 Aug	1.2
E. corymbosum 1	San Rafael Swell	Emery	1700	28 Sep	1.1
E. corymbosum 2	North of Moab	Grand	1270	28 Sep	1.0
E. corymbosum 3	Purgatory Flat	Washington	880	3 Nov	1.2
E. heracleoides 1	Soldier Summit	Utah	2270	8 Aug	2.7
E. heracleoides 2	Shingle Creek	Summit	2300	7 Sep	2.9
E. heracleoides 3	Clyde Creek	Wasatch	2520	18 Aug	3.0
E. jamesii 1	Cat Canyon	Carbon	1700	20 Jul	2.8
E. jamesii 2	East of Soldier Summit	Utah	2210	27 Aug	3.0
E. ovalifolium 1	Cat Canyon	Carbon	1700	11 Jun	1.3
E. ovalifolium 2	Terra	Tooele	1580	26 Jun	0.8
E. racemosum 1	Boulder Mountain	Garfield	2580	27 Aug	2.4
E. racemosum 2	Santaquin Canyon	Utah	1610	21 Sep	1.8
E. shockleyi	North of Bullfrog	Garfield	1150	28 Jun	1.3
E. umbellatum 1	East of Sigurd	Sevier	2150	26 Aug	1.4
E. umbellatum 2	Fishlake Pass	Wayne	2550	26 Aug	1.9
E. umbellatum 3	Red Canyon	Garfield	2330	27 Aug	2.6
E. umbellatum ssp. *majus*	Soldier Summit	Utah	2270	8 Aug	2.1
E. umbellatum ssp. *porteri*	Bald Mountain Pass	Summit	3480	7 Sep	2.6

[a] Multiply m by 3.3 to obtain feet.
[b] Multiply mg by 0.000035 to obtain ounces.

We used 4 replicates of 25 achenes for each collection-treatment combination in a completely randomized design. Achenes were placed in disposable plastic petri dishes (10 X 90 mm) on 2 blue germination blotters (Anchor Paper, St Paul, Minnesota) moistened with tapwater. Blotters were remoistened as needed. At the end of each chilling period and weekly during postchilling incubation, germinated achenes (radicle > 1 mm) were counted and removed. Germination was also scored weekly (in the light) during chilling in the 24-wk chilling treatment. At the end of post-chilling incubation for each chilling treatment, we scored remaining ungerminated achenes for viability using a cut test. Achenes that contained firm, yellow or white embryos with all parts intact were judged viable.

Results of the germination experiments were analyzed for each collection using one-way analysis of variance (ANOVA), with chilling duration as the independent variable and germination percentage after post-chilling incubation (based on viable seeds only) for each replication as the response variable. The data were arcsine-transformed to increase homogeneity of variance prior to the analysis. The Student-Neuman-Keuls test was used to separate means.

We used linear interpolation on germination time courses during 24 wk of chilling at 2 °C (36 °F) to calculate mean germination time (time to germination of 50% of viable seeds) for each collection. Mean germination time was then regressed on collection site elevation to test the prediction that collections from higher elevation habitats with longer winters would have longer germination times in the cold. We also regressed mean germination percentage after a 4-wk chill on collection site elevation, to test the prediction that collections from warmer, low elevation sites would germinate to higher percentages following a short chilling period than collections from colder, high elevation sites. *Eriogonum alatum* collections were excluded from these analyses because their achenes were completely nondormant after every chilling treatment and did not germinate at 2 °C (36 °F). Because *E. shockleyi* and *E. bicolor* collections were limited in quantity and included only in the 0- and 24-wk chilling treatments, they are absent from the 4-wk chilling response regression.

Results and Discussion

Achenes of the wild buckwheat species included in this study were either nondormant under the conditions of our experiment or became nondormant in response to chilling (Table 3). Given a sufficiently long chilling period, almost 100% of the viable achenes in each collection became germinable. There was no evidence for the presence of a fraction nonresponsive to chilling, nor was there evidence of any tendency for nondormant achenes to be induced into secondary dormancy by chilling. In general, the chilling period required for near-complete dormancy removal was shorter than or comparable to a period of winter chilling that might reasonably be expected in the habitat of origin for each collection.

The large achenes of the mid-elevation monocarpic perennial *E. alatum* showed a response pattern very different from that of the remaining species (Table 3). All 3 collections were completely nondormant without chilling, as well as after any length of chilling, but the achenes did not germinate while in the 24-wk chilling treatment (data not shown). This pattern suggests that *E. alatum* is primarily autumn-emerging. It presumably would germinate after the first autumn rains following its dispersal in late summer. In another experiment we showed that achenes of this species can germinate in 3 d or less at warm temperatures (Allen and others forthcoming).

Of the remaining species, only the cold-desert species *E. shockleyi* had achenes that were completely nondormant without chilling (Table 3). In contrast to *E. alatum*, however, its achenes germinated quickly (6 wk to 50%) under simulated winter conditions. This species is probably winter and spring-emerging, as it would not be likely to encounter enough moisture to germinate prior to winter in its dry habitat. *Eriogonum bicolor* is another cold desert species that appears to be adapted for winter and spring emergence. Its achenes were largely dormant without chilling, but germinated quickly in the cold (7 wk to 50%) and probably would have had a relatively short chilling requirement.

Collections of another desert species, *E. corymbosum*, showed germination response patterns that were probably related to habitat temperature. Two collections from low elevation, warm sites near Moab and St George germinated completely after a 4-wk chill and were relatively fast to germinate in the cold (5 and 8 wk to 50%, respectively), while a collection from a higher-elevation, more northerly site on the San Rafael Swell required 8 wk of chilling to break dormancy completely and was much slower to germinate in the cold (16 wk to 50%).

Collections of 2 other high desert-foothill species, *E. ovalifolium* and *E. jamesii*, contained a relatively large fraction of achenes that could germinate without chilling. All achenes of these species were rendered nondormant by an 8-wk chill. *Eriogonum ovalifolium* collections germinated to lower percentages without chilling (22% to 24%) than *E. jamesii* collections (50% to 65%), but *E. jamesii* collections germinated more slowly in the cold (14 to 16 wk to 50% compared to 10 to 11 wk to 50% for *E. ovalifolium*).

Eriogonum racemosum, an herbaceous perennial species of relatively mesic foothill sagebrush communities, showed high dormancy without chilling, but required only an 8-wk chill to become completely nondormant. Its germination rate in the cold was intermediate (10 to 14 wk to 50%).

Figure 2 • *Alpine sulfurflower buckwheat* (Eriogonum umbellatum *ssp.* porteri) *grown from seed collected on Bald Mountain Pass, Uinta Mountains, flowering in the senior author's rock garden in Elk Ridge, Utah.*

The remaining 3 species (*E. brevicaule*, *E. heracleoides*, and *E. umbellatum*) are characteristically found in mid to high montane habitats. They germinated to low percentages (< 20%) without chilling, and generally had long chilling requirements (≥ 12 wk for complete dormancy removal) and slow germination rates in the cold (> 15 wk to 50%).

The 5 collections of *E. umbellatum* represent 3 subspecies; they showed considerable variation in chilling requirement. The Red Canyon collection of subspecies *umbellatum* was the least dormant, requiring only an 8-wk chill to become completely germinable. The collection of subspecies *porteri* from an alpine tundra community in the Uinta Mountains was, perhaps not surprisingly, by far the most dormant in the experiment. It required a full 24 wk of chilling to lose dormancy completely and only germinated to slightly more than 50% during 24 wk in the cold.

When time to 50% germination at 2 °C (36 °F) was regressed on collection site elevation (for the 21 collections that germinated to 50% in the cold, that is, excluding *E. alatum*), the resulting regression line accounted for 74.4% of the variation, a highly significant result (Figure 4A). The slope was positive, meaning that as collection site elevation increased, time to 50%

TABLE 3

Mean germination percentage (expressed as percentage of total viable seeds) and mean total viability percentage (expressed as percentage of all seeds) for Utah Eriogonum

	Chilling period at 2 °C (36 °F) (wk)							
Collection	***0***	***4***	***8***	***12***	***16***	***24***	***Weeks to 50% germination at 2 °C (36 °F)***	***Mean viability (%)***
E. alatum 1	99 a [a]	100 a	100 a	100 a	100 a	100 a	— [b]	85
E. alatum 2	97 a	99 a	100 a	100 a	100 a	99 a	— [b]	73
E. alatum 3	95 a	100 a	100 a	100 a	100 a	100 a	— [b]	70
E. bicolor	6 b	— [c]	— [c]	— [c]	— [c]	100 a	7	62
E. brevicaule 1	0 e	17 d	52 c	84 b	95 a	99 a	16	87
E. brevicaule 2	6 d	42 c	64 b	83 a	92 a	95 a	15	89
E. corymbosum 1	5 c	58 b	97 a	100 a	98 a	100 a	16	90
E. corymbosum 2	63 b	96 a	99 a	100 a	100 a	100 a	5	97
E. corymbosum 3	19 b	96 a	100 a	100 a	100 a	100 a	8	89
E. heracleoides 1	1 e	11 d	43 c	69 b	99 a	100 a	17	85
E. heracleoides 2	3 e	5 e	19 d	52 c	80 b	99 a	19	85
E. heracleoides 3	15 c	24 c	55 b	68 b	98 a	97 a	17	69
E. jamesii 1	65 c	93 b	100 a	100 a	100 a	100 a	16	83
E. jamesii 2	50 c	84 b	100 a	100 a	99 a	97 a	14	82
E. ovalifolium 1	24 c	78 b	98 a	100 a	100 a	100 a	10	98
E. ovalifolium 2	22 c	61 b	99 a	100 a	100 a	100 a	10	85
E. racemosum 1	3 d	20 c	92 b	99 a	100 a	100 a	14	97
E. racemosum 2	7 c	42 b	97 a	98 a	100 a	100 a	10	92
E. shockleyi	100 a	— [c]	— [c]	— [c]	— [c]	100 a	6	67
E. umbellatum 1	6 d	22 c	77 b	98 a	100 a	100 a	14	88
E. umbellatum 2	5 d	35 c	77 b	97 a	100 a	100 a	16	85
E. umbellatum 3	5 c	34 b	98 a	100 a	100 a	100 a	13	90
E. umbellatum ssp. *majus*	18 c	23 c	52 b	92 a	100 a	100 a	16	81
E. umbellatum ssp. *porteri*	6 d	30 b	41 b	55 b	45 b	94 a	23	78

[a] Within a collection, germination percentage means followed by the same letter are not significantly different at the $P < 0.05$ level according to a Student-Newman-Keuls means separation test.

[b] No achenes germinated during chilling.

[c] No data for these conditions due to insufficient achenes.

germination in the cold also increased. This supported our hypothesis that collections from high elevation habitats with long winters would require longer to germinate under winter conditions than collections from warm, low elevation habitats. Most of the scatter around the regression line was in the middle elevation range, where species identity was as important as elevation in determining mean germination time in the cold (Table 3). Extreme values for the alpine *E. umbellatum* ssp. *porteri* did not influence the regression unduly; removing this point had no significant effect (data not shown).

Germination percentage after a 4-wk chill was negatively correlated with collection site elevation (Figure 4B). This result supported our hypothesis that collections from low elevation habitats with short winters would germinate to higher percentages in response to a short chill than collections from high elevation habitats. The relationship, though significant, was much weaker than the relationship between collection site elevation and mean germination time in the cold. Again, most of the scatter was in the mid-elevation range. Differences among species had an overriding effect on germination response to a 4-wk chill within this range (Table 3). The relationship between collection site elevation and germination percentage without chilling was not significant (data not shown), largely because low elevation collections belonging to different species showed such high variation in the fraction germinable without chilling (Table 3).

Our results clearly show that chilling is a primary regulator of dormancy status in achenes of wild buckwheats. Germination response to chilling was a function of both species identity and habitat. The species-specific patterns of response we observed are probably related to other features of species life history, such as life span, growth habit, flowering and fruiting phenology, and seedling ecology. The study species vary tremendously in all these features, yet the effect of habitat, specifically winter climate as indicated by elevation, on germination response to chilling was clearly observable across species.

We obtained similar results in our studies of the diverse Intermountain genus *Penstemon* Schmidel (Scrophulariaceae)(Kitchen and Meyer 1991; Meyer 1992; Meyer and Kitchen 1994b; Meyer and others 1995). While there were in a few instances species that did not follow the trend, the relationship between collection site climate and germination response was generally consistent across species.

One difference between *Penstemon* and *Eriogonum* is that most species of *Penstemon* have some mechanism for preventing full germination the first year following seed production, while the species of *Eriogonum* that we studied have no apparent carryover mechanism. Lack of a seed bank carryover mechanism is often more characteristic of long-lived shrubs (Meyer and others 1989; Meyer and Monsen 1991) than of herbaceous perennials. Most of our study species are woody and long-lived, but even the herbaceous species (*Eriogonum alatum* and *Eriogonum racemosum*) had no apparent carryover mechanism.

It is possible that nondormant achenes of some wild buckwheat species are light-requiring and might therefore form persistent buried seed banks. We did not examine this possibility in our experimental design. For big sagebrush (*Artemisia tridentata* Nutt. [Asteraceae]), most achenes lost their light requirement during chilling, but a very small fraction remained light-requiring and thus potentially persistent (Meyer and others 1990).

It is also possible that apparently dormant achenes of some wild buckwheat species might have been only conditionally dormant at our testing temperatures and able to germinate at higher temperatures. To date, the only Intermountain species known to show this pattern is a fall-dispersing shrub, rubber rabbitbrush (*Chryothamnus nauseosus* (Pallas) Britt. [Asteraceae]) (Meyer and others 1989). For primarily summer-dispersing species like wild buckwheats, increased dormancy at high temperatures would be more likely.

Dormancy in *Eriogonum* appears to function predictively to time germination during the year following production. In most of the species studied, the response to chilling would result in late winter germination and early spring emergence in the habitat of origin, though there is a possibility for fall emergence in species that produce a nondormant fraction. Because we tested our collections only once, after achenes had been in dry storage in the laboratory for 2 to 5 mo, we do not know whether after-ripening under dry conditions plays any role in dormancy loss for these species.

Practical Implications

Wild buckwheat species represent an untapped source of easily propagated drought-tolerant ornamentals ideal for home xeriscapes, as well as providing cover and diversity in reclamation seedings. They may be direct-seeded in late fall for spring emergence over much of the Intermountain West (Stevens and others 1996). Many wild buckwheats are early-successional species that establish readily from seeds and grow quickly, as long as competition from weeds or perennial grasses is kept to a minimum (Ratliffe 1974; Tiedemann and Driver 1983; Zamora 1994; Stevens and others 1996; Meyer forthcoming).

Wild buckwheats are also readily produced as nursery stock. Shaw (1984) reported that *E. heracleoides* could be successfully produced as 1+0 bareroot stock, but had to be lifted carefully because of the taprooted habit. Other species could probably be produced in a similar system. In container production, the taprooted habit necessitates the use of book planters or tube containers such as those used for producing conifer seedlings. Nondormant lots may be direct-sown, while lots requiring chilling may be sown as chilled seed or as young germinants (Landis and Simonich 1984). Seedlings of many species grow rapidly and may even flower in small containers. Plants should not be held in small containers for more than a few months.

Figure 3 • *Pretty buckwheat* (Eriogonum bicolor) *flowering in the wild near Capitol Reef National Park.*

Wild buckwheat achenes are generally easy to collect, clean, and germinate. Results of the research presented here may be used to "guesstimate" chilling requirements for wild buckwheat seedlots of unknown dormancy status. Collections from habitats with long, snowy winters are likely to have proportionately long chilling requirements, while collections from dry desert habitats are likely to be nondormant or to have short chilling requirements. Collections from middle elevation habitats are likely to have chilling requirements of intermediate length. Species-specific responses are also important, especially if the collection is from a middle elevation site. We have included data for many common, widely distributed species that can be used as a guide to probable chilling response. For collections of species not included here, habitat is the best guide.

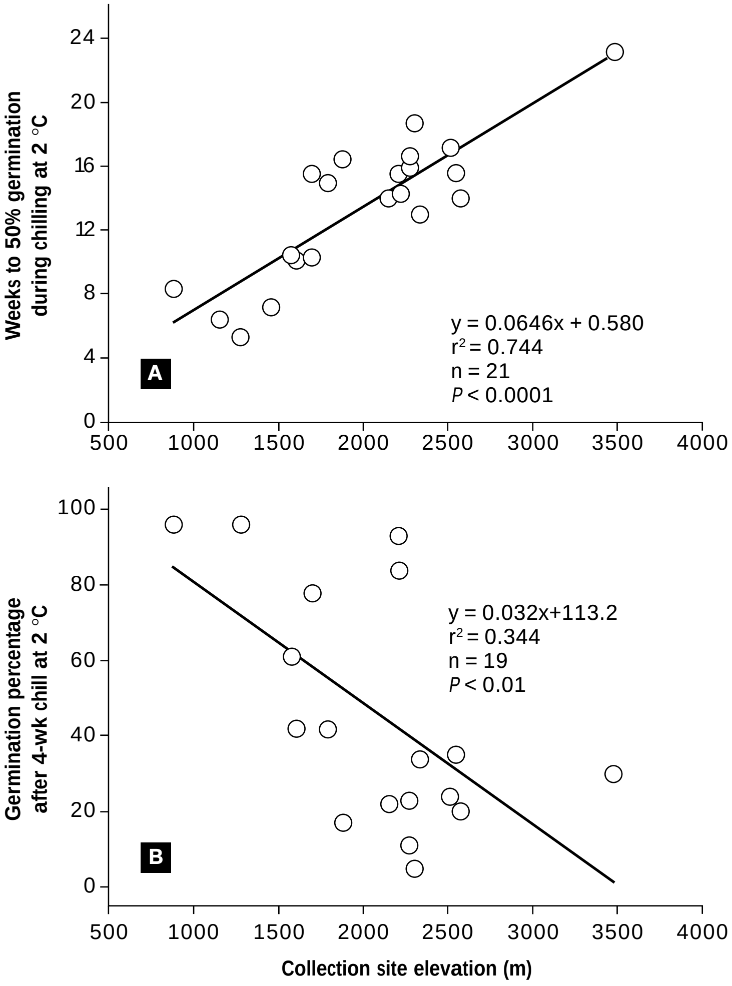

Figure 4 • *(A) Relationship between collection site elevation and weeks to 50% germination at 2 °C (36 °F) for 21 collections of* Eriogonum *belonging to 9 species. (B) Relationship between collection site elevation and germination response to a 4-wk chill at 2 °C (36 °F) followed by 4 wk with a daily alternating temperature and photoperiod (12 h dark at 10 °C [50 °F] and 12 h light at 20 °C [68 °F]) for 19 collections of* Eriogonum *belonging to 7 species. (Multiply m by 3.3 to obtain feet).*

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