Autecology of *Erythronium grandiflorum* in western Canada

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Abstract: Habitat requirements of the yellow glacier lily, *Erythronium grandiflorum* Pursh, were studied at 38 sites in southern British Columbia and southwestern Alberta. At each site we recorded densities of *E. grandiflorum* growth stages from seedling to flowering, environmental characteristics of the site, and percent cover of associated plant species. We carried out detrended correspondence analysis (DCA) of the sites based on cover of associated species, and examined rank correlations between site environmental variables and site ordination scores. Variation among sites was related primarily to elevation and the presence of deciduous vs. coniferous trees. All growth stages of *E. grandiflorum* were less abundant in coniferous forests than in open areas or sites with deciduous trees, suggesting that evergreen canopies restrict the species on many sites where it could otherwise grow. Although *E. grandiflorum* populations were most commonly found in subalpine meadows, they flowered more abundantly in low-elevation populations. Recruitment was frequent, with seedlings occurring at many sites; we also showed that detached bulb segments can give rise to new ramets. The present widespread distribution of *E. grandiflorum* may derive from a post-glacial period with extensive meadow habitat that was favourable for rapid spread.

Key words: canopy cover, elevation, yellow glacier lily, post-glacial migration, subalpine meadows.

Résumé : Les auteurs ont étudié les caractéristiques des habitats nécessaires au lis jaune des glaciers, l'*Erythronium grandiflorum* Pursh, sur 38 sites du sud de la Colombie Britannique et du sud-ouest de l'Alberta. Sur chaque site, ils ont enregistré la densité des stades de développement des *E. grandiflorum*, de la plantule à la floraison, ainsi que les caractéristiques environnementales du site, et le pourcentage de couverture des plantes associées. Ils ont effectué des analyses par correspondances hors-tendances (DCA) des sites, basées sur la couverture des espèces associée, et ils ont examiné l'ordination des corrélations entre les variables environnementales du site et les données d'ordination du site. La variations entre les sites est surtout reliée à l'élévation et à la présence d'arbres décidus vs des conifères. Tous les stades de développement de l'*E. grandiflorum* sont moins abondants dans les forêts conifériennes que sur les stations ouvertes, ou les sites avec des arbres décidus, ce qui suggère que les canopées conifériennes restreignent l' espèces sur plusieurs sites où elle pourrait par ailleurs se développer. Bien que les populations de l'*E. grandiflorum* se retrouvent plus communément dans les prairies sub-alpines, elles fleurissent plus abondamment dans les populations de basses élévations. Le recrutement est fréquent, avec la présence de plantules sur plusieurs sites; les auteurs montrent également que des segments de bulbes détachés peuvent donner de nouvelles ramètes. La large distribution actuelle de l'*E, grandiflorum* pourrait provenir de la période post-glaciaire comportant de grands habitats de prairie, ce qui était favorable à une rapide dispersion.

Mots clés : canopée, élévation, lis jaune des glaciers, migration post-glaciaire, prairies sub-alpines.

[Traduit par Rédaction]

Introduction

Factors controlling the distribution and abundance of species may be proximal or historical. The relative importance of current environmental conditions, species interactions, disturbance factors, and long-past events is a central, but largely unresolved, ecological question. Climate and species distributions have changed dramatically since the last glaciation (Ritchie 1987) and it is very plausible that many species exhibit lags in response to climate change and thus non-equalibrium distributions (e.g., Allen et al. 1996). Case studies of individual species can make valuable contributions to generalizations about the factors controlling distribution and abundance.

Erythronium grandiflorum Pursh, the yellow glacier lily, is widespread in the mountains of western North America, ranging from northern California and New Mexico to southern British Columbia and southwestern Alberta. It has a much larger range than other species of *Erythronium* in western North America, many of which are localized endemics (Applegate 1935; Shevock et al. 1990; Allen 1993), and occurs in a wide diversity of habitats including grasslands, various types of forests, and subalpine meadows (Hitchcock et al. 1969; Kuijt 1982; Fritz-Sheridan 1988; Rigney 1995). It is a spring ephemeral, flowering soon after snowmelt and senescing within two months after emergence (Caldwell 1969; Fritz-Sheridan 1988; Rigney 1995).

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Flowering individuals of *E. grandiflorum* have two basal leaves and most commonly a single, nectar-bearing, yellow flower; nonflowering plants usually have a single leaf. Bumblebees (*Bombus* spp.) appear to be the most common pollinators (Pojar 1974; Thomson and Stratton 1985; Fritz-Sheridan 1988). The capsules contain 20–60 seeds, each approximately 5 mg (Fritz-Sheridan 1988; Weiblen and Thomson 1995). The seeds are dispersed from the capsules by wind or other mechanical disturbance, in contrast to those of *Erythronium americanum* and *Erythronium japonicum*, which bear elaiosomes and are ant-dispersed (Handel et al. 1981; Ohkawara et al. 1996). Weiblen and Thomson (1995) reported a mean seed dispersal distance for *E. grandiflorum* of only 0.33 m with >95% of seeds falling within 0.9 m of the parent plant. The plants have an elongated corm-like bulb, commonly with an attached chain of segments representing bulb remnants from previous years. This unusual morphology has also been found in *E. japonicum* (Ogura 1952; Kawano et al. 1982) and *E. montanum* (Antos and Zobel 1984; Antos 1988). Although vegetative spread has not been recorded for *Erythronium grandiflorum*, we show in this paper that the bulb segments are able to form new ramets if detached, as also occurs in *E. japonicum* (Kawano et al. 1982).

Erythronium grandiflorum bulbs are an important food resource for both grizzly bears and small mammals, which may consequently have a major impact on the spatial structure and dynamics of *E. grandiflorum* populations (Zager 1980; Hamer et al. 1991; Thomson et al. 1996; Tardiff and Stanford 1998). Aboriginal peoples also excavated the bulbs, which were an important food source for many groups (Turner 1997; Loewen 1998). *Erythronium grandiflorum* has been the subject of numerous studies ranging from microsite distribution patterns to photosynthetic physiology (e.g., Hamerlynck and Smith 1994; Thomson et al. 1996); the pollination biology of this species has been especially well studied (e.g., Thomson and Stratton 1985; Thomson and Thomson 1989; Cruzan 1990; Holsinger and Thomson 1994; Rigney 1995). However, little is known about the overall habitat requirements of this wide-ranging species and no previous studies have examined *E. grandiflorum* habitats in Canada. Our objectives were to 1) document the stage structure of *E. grandiflorum* populations, 2) determine if segments attached to the bulb can form new ramets, 3) determine habitat characteristics and plant species composition of sites occupied by *E. grandiflorum* in British Columbia and Alberta, 4) relate the stage structure of populations to habitat characteristics, and 5) make inferences about the factors controlling the distribution and abundance of *E. grandiflorum*.

Methods

Field and laboratory procedures

We sampled 38 sites (21 sites in 1996 and 17 sites in 1997) distributed throughout most of the range of *Erythronium grandiflorum* in British Columbia and Alberta (Fig. 1). Within the constraints imposed by accessibility and flowering times, sites were chosen to represent a range of elevations and habitat types. All populations were sampled while *E. grandiflorum* was in flower to ensure consistency of sampling with respect to both species cover and *E. grandiflorum* characteristics.

At each site, a 15 × 20 m (occasionally 10 × 30 m) plot was centrally located within an area of uniform physiognomy and *E. grandiflorum* phenology. Ten 1 × 1 m quadrats, evenly spaced along two transects (or one central transect in 10 × 30 m plots), were placed in each plot. Percent cover of all herbaceous and shrub species was estimated within each quadrat. Diameter at breast height was recorded for all trees >1.5 m tall in the entire plot; cover of smaller trees was estimated in the ten quadrats. Nomenclature follows Hitchcock and Cronquist (1973).

Within quadrats we counted all *Erythronium* individuals, assigning them to the following growth stages: seedling, one-leaf nonflowering, two-leaf nonflowering, and flowering (separating plants with one, two, three, four, and more than four flowers). We also counted aborted flowers and herbivore-damaged scapes. For two plants per quadrat (those nearest the two corners away from the transect line) we recorded length and width of the longer leaf and calculated leaf area (assuming the leaves to be elliptic). Leaf area in *E. japonicum* (Kawano et al. 1982) is strongly correlated with total plant biomass, and we used it as an index of plant size in *E. grandiflorum*.

For each plot we recorded elevation, aspect (coded for analysis as $A = \cos(202.5° - \text{azimuth from true north}) - 1$), and slope angle (degrees from horizontal) in addition to disturbances such as grazing or digging by animals. Within each quadrat, we measured litter depth and estimated percent cover of litter, wood, bare soil, bare (or thinly lichen- or moss-covered) rock, and tree bases. For each site we calculated an index of substrate rockiness (Thomson et al. 1996) by averaging 40 depth measurements (from the corners of the 10 quadrats) obtained by inserting an aluminum pole into the ground until it reached rock or a depth of 40 cm.

To examine soil properties, approximately 100 g of soil was taken from bulb depth (range 4–32 cm, mean = 13.9 cm) in each quadrat. We measured pH of each sample on the day of collection using an Oakton pHTestr 2 portable pH meter. The ten samples from each site were then composited, air-dried, and used for analysis of particle size and organic matter content. Sieves of mesh sizes 2, 1, 0.5, 0.25, 0.125, 0.075, and 0.038 mm were used. The smallest mesh sieve separated coarse silts from finer silts and clays (Day 1983). Organic matter content was determined using the loss-on-ignition method (McKeague 1978). Two subsamples from the bulk sample for each site were ashed; if these differed by >10%, a third subsample was taken and the average of the two closest values (which were always within 10%) was used.

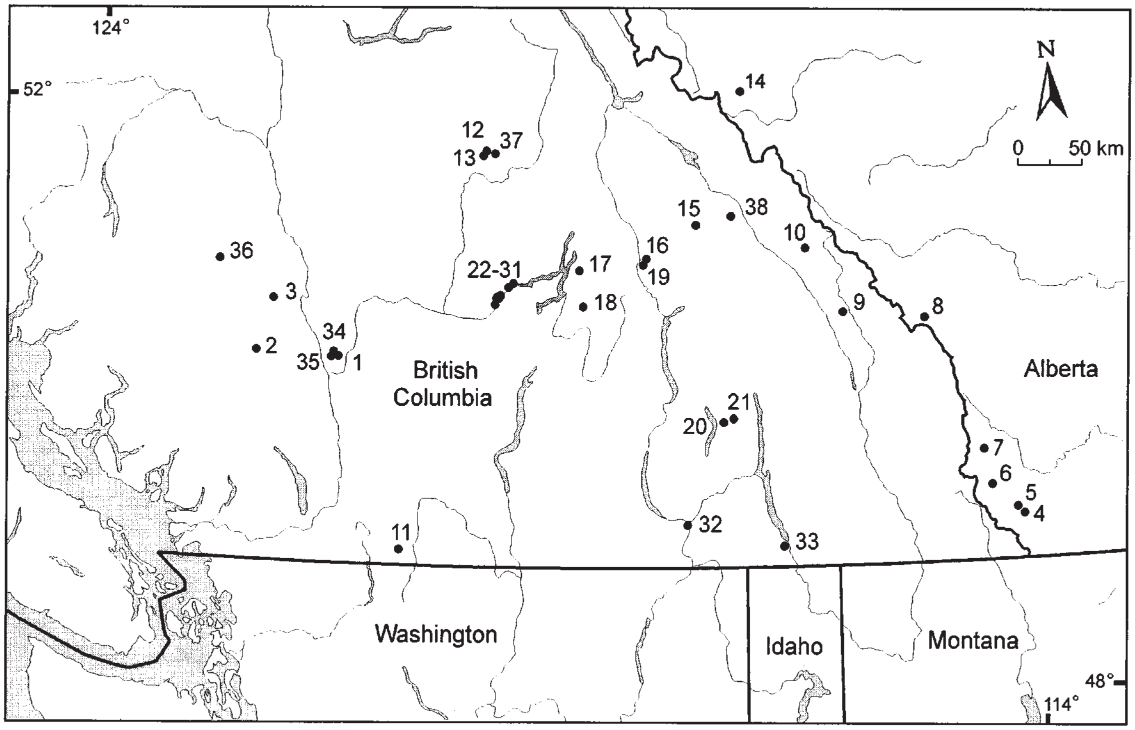
To determine if segments attached to the bulb could form new ramets, we collected bulbs at Trophy Meadows in Wells Gray Provincial Park (elevation 1950 m) on August 9, 1996 and planted five sets of detached segments in a cleared area at Trophy Meadows and 10 sets of segments in a garden near Clearwater, British Columbia (elevation 450 m). A set consisted of the chain of usually three to six segments attached to a single bulb.

Data analysis

To examine patterns of variation among the 38 sites based on species composition, we used DCA, a widely used ordination method (ter Braak 1995), implemented with PC-ORD for Windows version 3.09 (McCune and Mefford 1997). Cover values for each species were averaged over the 10 quadrats at each site. We constructed ordinations for both percent cover data and presence–absence data; because these were very similar, we present only results based on cover data. Prior to analysis, all species occurring in only one site were deleted (Gauch 1982) and cover data were log transformed (ter Braak 1995; McCune and Mefford 1997), which gave a much better fit between distances in the ordination space and distances in the original, unreduced space (R^2 calculated using PC-ORD).

To interpret ordination patterns we examined rank correlations between environmental variables and ordination axis scores for each site. To evaluate the success of *E. grandiflorum* populations in different kinds of habitats (as inferred from species composition), we examined correlations between the densities of various growth

Fig. 1. Sites sampled for *Erythronium grandiflorum* populations in British Columbia and Alberta.



stages and ordination scores. Because most variables were not normally distributed (as indicated by the Wilk-Shapiro statistic), we used Kendall's coefficient of rank correlation, τ (McCune and Mefford 1997). In all, we used 14 environmental and 9 *E. grandiflorum* quantitative variables for the analyses; some variables were eliminated prior to analysis because they were highly correlated with other variables or contained too few non-zero values to be meaningful (see Loewen 1998 for details of variable selection and derivation). We used Spearman's rank correlations to examine directly the relationship of environmental variables to measures of *E. grandiflorum* density and vigour. Calculations were performed using Statistix for Windows version 1.0 (Analytical Software, Tallahassee, Florida). Because of the many comparisons involved, only correlations significant at $P < 0.01$ were interpreted.

Because the densities of some growth stages of *E. grandiflorum* were not linearly related to elevation, we compared high- and low-elevation sites directly using the Mann–Whitney U test (Sokal and Rohlf 1995). Ten low-elevation sites representing meadows to deciduous woods (sites 1, 22, 24–26, 28–30, 34–35 in Fig. 1) were compared with 13 high-elevation, subalpine meadow sites (sites 11–13, 15–21, 36–38). Sites were selected using a TWINSPAN classification of all sites (Loewen 1998).

Results

Erythronium grandiflorum population characteristics

Density and growth-stage structure of *E. grandiflorum* populations varied greatly among sites (Table 1). Seedling densities (means of 10 quadrats per plot) ranged from 0–60.7 seedlings per metre squared among sites. Seedlings were highly variable in number, both among plots and among quadrats in a plot, and often occurred in tight groups resulting from a single capsule. Density of one-leaf, nonflowering plants averaged 130.3 plants per metre squared over all sites; over 50% of the sites had more than 100 plants per metre squared. Densities of two-leaf, nonflowering plants were much lower; only 6 sites had more than 15 plants per metre squared. Flowering plant density averaged 28.6 plants per metre squared. At all sites, the great majority of flowering plants bore one flower; on average 6% of flowering plants had multiple flowers. Plants with three or more flowers were rare and only one plant with more than four flowers was found. Percent cover of *E. grandiflorum* averaged 25% (a range of 5–64%). Average leaf length varied considerably among populations (range 9.0–29.5 cm, mean = 18.1 cm).

Plants emerged from bulb segments at both planting sites, demonstrating that detached segments can yield new ramets. At Trophy Meadows, two of the five sets of segments produced plants (three in total, one of which had two leaves). At the low-elevation garden, 10 sets of segments yielded three plants in the first year after planting and eight plants in the second year (one to six plants per set, indicating the presence of multiple latent meristems).

Ordination patterns and environmental gradients

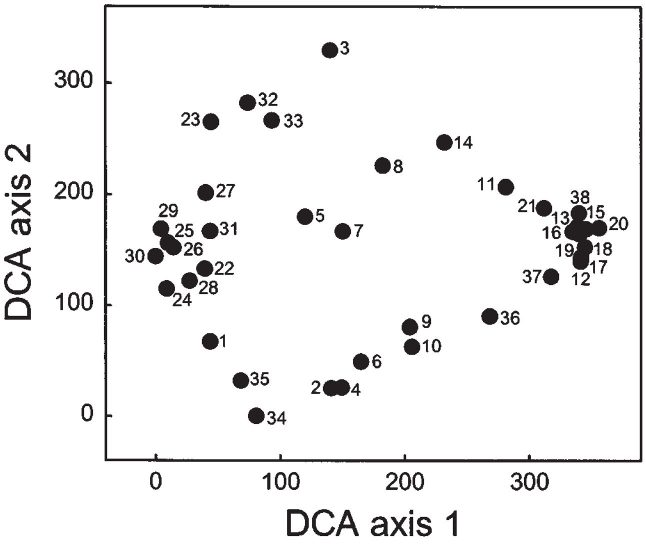
The first axis of the DCA ordination (Fig. 2) represented a major vegetation gradient from low-elevation grasslands to subalpine meadows; this axis showed a strong positive correlation with elevation (Table 2; Fig. 3*a*). Soil pH, texture, and organic content were also correlated with the first ordination axis; high-elevation sites had coarser-textured, more acid soils with higher organic matter (Table 2; Fig. 3*b* and 3*c*). Litter depth and cover showed significant negative correlations with the first axis (Table 2; Fig. 3), indicating higher values for these attributes in low-elevation grasslands than in subalpine meadows. Two clusters of sites are apparent in Fig. 2. Subalpine sites (12–13, 15–21, and 37–38), although widely dispersed geographically (Fig. 1), possessed a similar suite of species and formed a tight cluster on the right side of the ordination (Fig. 2). A somewhat

Table 1. Means and ranges of abundance of *Erythronium grandiflorum* growth stages at 38 sites and rank correlations (Kendall's τ) between abundances and the first and second axis scores of the DCA ordination (Fig. 2).

Variable	Mean	Range	Axis 1	Axis 2
Density of seedlings (number per metre squared)	13.4	0–60.4	0.229	–0.093
Density of one-leaf plants (number per metre squared)	130.3	15.1–388.4	–0.098	0.021
Density of two-leaf, non-flowering plants (number per metre squared)	12.8	0.3–106.0	0.409*	0.013
Density of flowering plants (number per metre squared)	28.6	0.8–90.0	–0.201	–0.318*
Proportion of all flowering plants with multiple flowers	0.06	0–0.41	–0.161	–0.428*
Proportion of all plants (excluding seedlings) that were flowering	0.17	0.02–0.43	–0.186	–0.465*
Proportion of two-leaf, non-flowering plants among all plants (excluding seedlings)	0.08	0.01–0.24	0.451*	0.081
Ratio of seedlings to flowering plants	0.62	0–2.18	0.235	0.064

$^*P < 0.01$ ($\tau = 0.292$).

Fig. 2. DCA ordination of 38 *Erythronium grandiflorum* sites based on log-transformed cover data for 157 taxa. Eigenvalues are 0.638 for the first axis and 0.375 for the second axis. Sites are numbered as in Fig. 1.

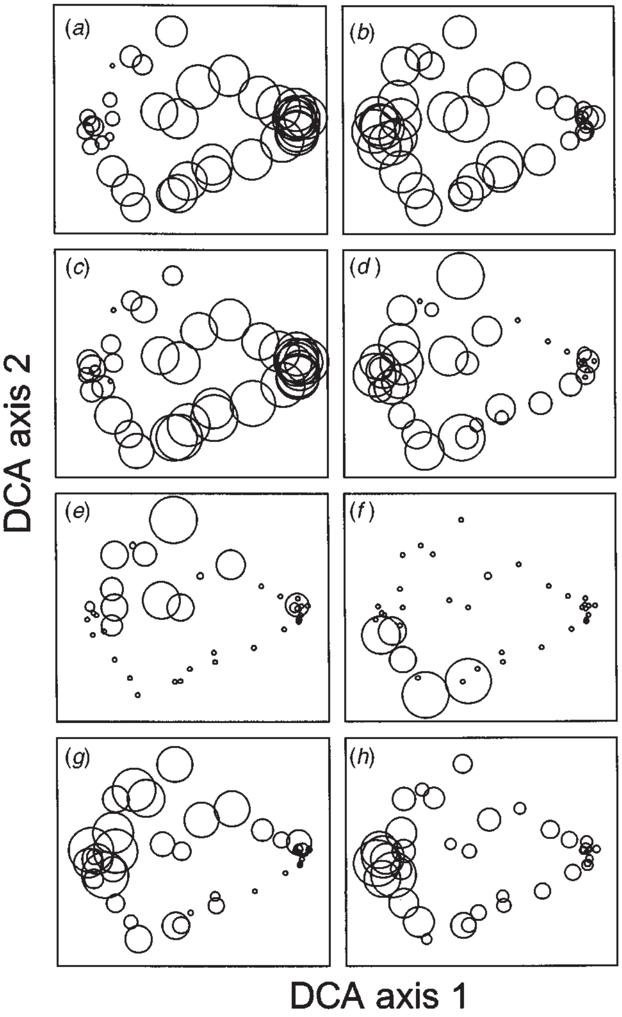


more heterogeneous group of low-elevation sites from the Chase and Adams River areas of central British Columbia (sites 22–31), with many species typical of low-elevation grasslands, formed a group on the left side of the ordination; these varied from *Pseudotsuga menziesii* forest to open shrub-dotted meadows. These low-elevation sites had greater cover of grasses and shrubs (Fig. 3*g* and 3*h*) and also a greater percentage of introduced species, as indicated by significant negative correlations of these variables with the first ordination axis (τ = –0.673, –0.492, and –0.640 respectively). Sites with intermediate scores on the first ordination axis represented a diversity of habitats including mid-elevation meadows, *Pseudotsuga menziesii* stands, forests of *Picea glauca*, *Pinus contorta*, or wind-stunted *Populus tremuloides*, and steep avalanche chutes.

The second axis of the ordination was related to tree species composition; this axis was positively correlated with basal area of coniferous trees but negatively correlated with basal area of deciduous trees (Table 2; Fig. 3*e* and 3*f*). None of the abiotic site factors measured in this study were significantly ($P < 0.01$) correlated with the second axis. The third ordination axis showed no significant correlations with site variables.

Beta diversity was high across these sites because of the large geographical region and elevational range sampled.

Fig. 3. Environmental and stand characteristics of 38 *Erythronium grandiflorum* sites plotted on the DCA site ordination (Fig. 2): (*a*) elevation, (*b*) soil pH, (*c*) soil texture (higher values indicate coarser soils), (*d*) litter depth (cm), (*e*) basal area of coniferous trees, (*f*) basal area of deciduous trees, (*g*) percent cover of shrubs, and (*h*) percent cover of grasses. Circle area is proportional to the value of the variable. Correlations between the variables and ordination axes are given in Table 2 or in the text.



Only 59 of the 157 species sampled occurred in more than five sites; few species were common to both low-elevation grasslands and subalpine meadows. Of the 59 most frequent

Table 2. Rank correlations (Kendall's τ) between environmental variables and first and second axis scores of the DCA ordination (Fig. 2) at 38 *Erythronium grandiflorum* sites.

Variable	Axis 1	Axis 2
Elevation	0.687*	0.084
Latitude	0.127	0.007
Longitude	–0.098	–0.189
Slope angle	–0.001	–0.132
Slope aspect (higher values indicate warmer aspects)	0.120	–0.157
Soil pH	–0.620*	–0.113
Soil texture (higher values indicate coarser soils)	0.523*	–0.224
Soil organic matter content	0.474*	–0.061
Rockiness index	0.252	0.110
Litter depth	–0.486*	–0.161
Percent cover of litter	–0.421*	0.034
Percent cover of wood	–0.294	0.052
Basal area of coniferous trees	–0.002	0.502*
Basal area of deciduous trees	–0.279	–0.323*

*$P < 0.01$ ($\tau = 0.292$).

Fig. 4. Abundance of growth stages in 38 *Erythronium grandiflorum* populations plotted on the DCA site ordination (Fig. 2): (*a*) density of seedlings (seedling per metre squared), (*b*) density of one-leaf plants, (*c*) density of flowering plants, (*d*) proportion of flowering plants with multiple flowers, (*e*) proportion of flowering plants among all plants (excluding seedlings), (*f*) proportion of two-leaf, non-flowering plants among all plants (excluding seedlings). Circle area is proportional to the value of the variable. Correlations between the variables and ordination axes are given in Table 1.

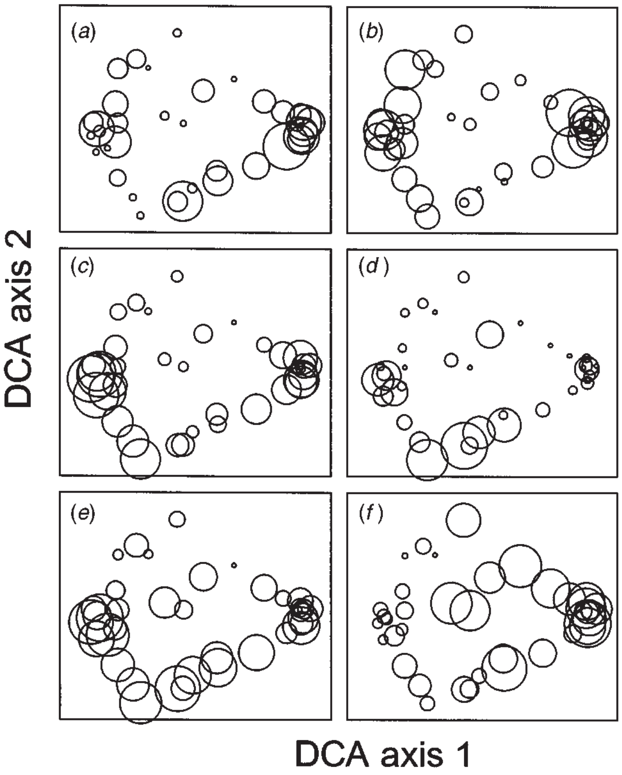
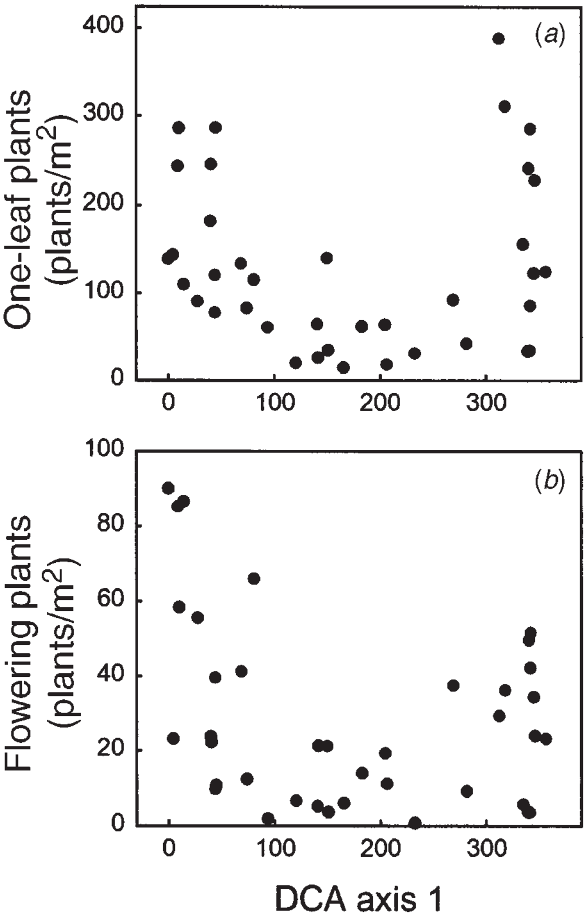


Fig. 5. Density of (*a*) one-leaf plants and of (*b*) flowering plants versus axis 1 site scores from the DCA ordination (Fig. 2) for 38 *Erythronium grandiflorum* sites.

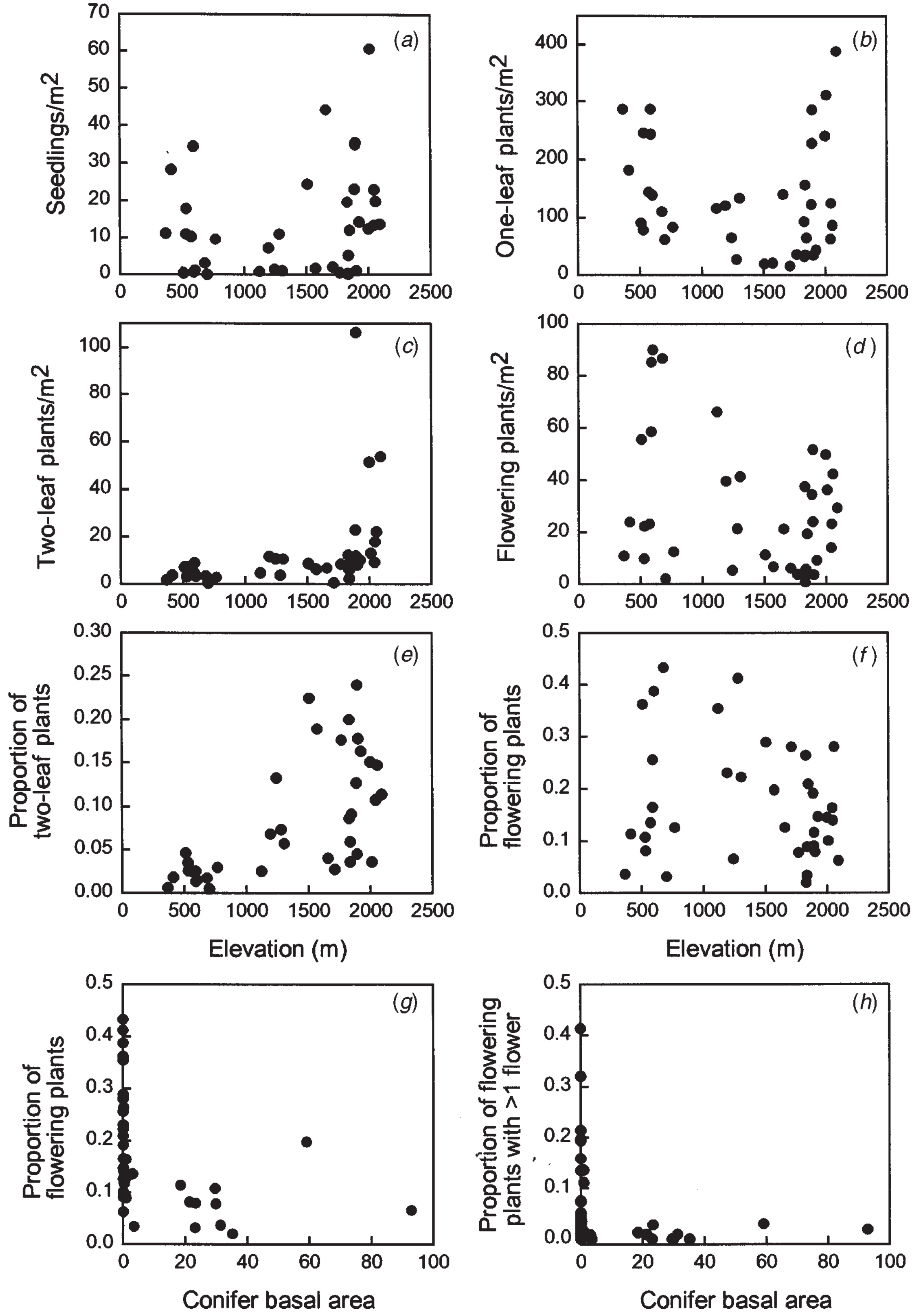


species, 45 showed significant ($P < 0.01$) rank correlations with the first axis and only 13 were significantly correlated with the second axis.

Relationships of *Erythronium grandiflorum* to the environment

Various growth-stage characteristics of the sampled *E. grandiflorum* populations were strongly related to ordina-

Fig. 6. Abundance of growth stages in *Erythronium grandiflorum* populations versus site factors (elevation for *a*–*f*, conifer basal area for *g*–*h*): (*a*) density of seedlings, (*b*) density of one-leaf plants, (*c*) density of two-leaf, non-flowering plants, (*d*) density of flowering plants, (*e*) proportion of two-leaf, non-flowering plants among all plants (excluding seedlings), (*f*) proportion of flowering plants among all plants (excluding seedlings), (*g*) proportion of flowering plants among all plants (excluding seedlings), and (*h*) proportion of flowering plants with multiple flowers.



tion axes, indicating relationships to major habitat gradients (Table 1; Fig. 4). Both number and proportion of two-leaf, non-flowering plants showed significant positive rank correlations with the first axis, indicating that these plants were most abundant in high-elevation meadows. Densities of one-leaf, nonflowering plants (the vast majority of all plants) and of flowering plants were not significantly correlated with the first ordination axis, but rather were bimodally distributed; sites on both the left and right sides of the ordination had high values for both of these variables, whereas sites lying between these invariably had low values (Fig. 5). The number of flowering plants, proportion of plants that were flowering, and proportion of flowering plants with more than one flower were all negatively correlated with the second axis (Table 1; Fig. 4), indicating that sites lacking conifer canopies were more favourable for flowering.

Relationships between population and site variables (Fig. 6) generally confirmed interpretations derived using ordination axes, although there were some differences. The density of one-leaf plants had a bimodal relationship with elevation, as it did with the first ordination axis (Fig. 5*a* and 6*b*). However, the first axis evidently does not solely reflect elevation, as flowering plant density showed a different pattern with elevation than with Axis 1 of the ordination (Fig. 5*b* and 6*d*). Both density and proportion of two-leaf, nonflowering plants were strongly correlated with elevation (Fig. 6*c* and 6*e*; $r_s = 0.671$ and 0.678, respectively), whereas seedling densities were not correlated with elevation (Fig. 6*a*) or any other measured site factor. Flowering was negatively correlated with conifer abundance ($r_s = -0.673$ for proportion of plants flowering and –0.515 for proportion of flowering plants with multiple flowers) (Fig. 6*g* and 6*h*), confirming our interpretation of its correlation with the second ordination axis.

When low- and high-elevation populations were compared directly, some characteristics showed significant differences that were not apparent with the entire data set because of non-linear relationships with elevation and with the first ordination axis. Density of flowering plants, proportion of plants flowering, proportion of flowering plants with multiple flowers, and leaf area were all higher in low-elevation sites, suggesting that plants are more vigorous at low elevations (Table 3). In contrast, the ratio of seedlings to flowering plants was significantly larger at high elevations (Table 3). The density of one-leaf plants (i.e., most plants) was very similar between high- and low-elevation sites.

Discussion

Population densities and reproduction

We found total density of *E. grandiflorum* to be higher at high- and low-elevation sites than at intermediate elevations, indicating that mid-elevation sites provided the least favourable conditions for this species. The abundance of trees at middle elevations appears to be the critical factor reducing the density of *E. grandiflorum*. Many species are displaced or reduced in abundance in central parts of an environmental gradient by species interactions, a situation that has long been recognized (Whittaker 1956).

Although *E. grandiflorum* is generally considered typical of subalpine meadows, we found it at equally high densities in low-elevation meadows, shrubfields, and deciduous woodlands. Furthermore, plants appeared to be more vigorous at low elevations, which probably reflected more favourable climatic conditions (e.g., warmer temperatures) and less rocky soils. The higher proportions of both flowering plants and plants with multiple flowers indicated that conditions for blooming are more favourable at low elevations. Conversely, two-leafed, non-flowering plants were much more abundant in high-elevation meadows. These plants may represent a large non-flowering stage or (as our observations at a number of sites suggested) they may be plants of flowering size that have aborted flower development. Floral abortion may account for the relatively high abundance of two-leaf, non-flowering plants in subalpine meadows, reinforcing the suggestion that environmental conditions at high elevations are suboptimal for flowering.

Although plants at low-elevation sites were larger and had higher rates of flowering, we found the ratio of seedlings to flowering plants to be significantly greater at high elevations. Thus, the low-elevation sites, where seed production is probably highest, are not the most favourable for seedling establishment. The greater amounts of litter at these sites may result in fewer safe sites for seedlings, although across-site correlations between seedling abundance and litter depth or cover were not significant. Rapid drying of surface soils may also be an important factor limiting seedling establishment at low elevations.

We have shown here that bulb-appendages in *E. grandiflorum* can act as vegetative propagules when mechanically separated from the parent plant. In this respect, this species resembles *E. japonicum*, which has similar bulb-appendages (Kawano 1982, 1984; Kawano and Nagai 1982; Kawano et al. 1982). It seems likely that vegetative reproduction occurs only rarely in *E. grandiflorum* without mechanical intervention; although we observed many plants during digging at the sites, we saw none that derived from a distinct appendage. However, the formation of new ramets from bulb appendages may be common following disturbance by digging, which could easily detach the appendages.

Effects of disturbance

Digging was likely an important form of disturbance in many habitats containing *E. grandiflorum*. Both indigenous peoples and grizzly bears harvested the bulbs and could have caused disturbance over large areas of meadow (Loewen 1998; Tardiff and Stanford 1998; Peacock and Turner 1999; Turner et al. 2000). Fossorial rodents that create tunnel systems, such as pocket gophers (*Thomomys talpoides*), preferentially consume below-ground storage organs and may cause extensive soil disturbance in some meadows (Huntly and Inouye 1988). Although consumption of bulbs would negatively affect population density, the associated disturbance from excavation may have had an overriding positive influence. In a subalpine meadow in Glacier National Park, Montana, higher levels of ammonium and nitrate occurred in soils disturbed by digging; *E. grandiflorum* growing in these soils had higher amounts of tissue nitrogen and water soluble carbohydrates in bulbs, higher photosynthetic rates, and higher seed production (Tardiff and Stanford 1998; Young 1998). Reduction in competition due to digging may have accounted for the higher soil nutrient levels and increased

Table 3. Comparisons of *Erythronium grandiflorum* populations between 10 low elevation (x = 757 m, SD = 320 m) sites (meadows, shrublands, and deciduous woods) and 13 high elevation (x = 1937 m, SD = 90 m) subalpine meadows.

	Low elevation		High elevation		
Variable	Mean	SD	Mean	SD	P
Density of seedlings (number per metre squared)	8.7	12.4	20.2	16.4	0.0628
Density of one-leaf plants (number per metre squared)	156.7	62.8	165.3	115.3	0.8282
Density of two-leaf, non-flowering plants (number per metre squared)	6.2	3.1	26.0	28.9	0.0048
Density of flowering plants (number per metre squared)	57.0	25.0	27.0	17.1	0.0092
Proportion of all flowering plants with multiple flowers	0.10	0.09	0.02	0.03	0.0070
Proportion of all plants (excluding seedlings) that were flowering	0.7	0.11	0.13	0.07	0.0084
Proportion of two-leaf, non-flowering plants among all plants (excluding seedlings)	0.03	0.02	0.11	0.06	0.0007
Ratio of seedlings to flowering plants	0.25	0.39	0.76	0.52	0.0070
Leaf area (cm^2)	62.6	26.0	40.5	13.4	0.0170

Note: Significance was determined with the Mann–Whitney *U* test.

plant growth. Hughes (1992) showed experimentally that removal of co-occurring vegetation dramatically increased the local distribution and abundance of *E. americanum*. Disturbance by digging may also favour seedling establishment; seedlings of *E. grandiflorum* establish readily on mineral soil exposed by burrowing animals (Caldwell 1969). Population density could also increase as bulb appendages separated during digging form new ramets. Although we commonly observed microdisturbances created by digging in high-elevation meadows, they were almost absent at the low-elevation sites sampled, reflecting changing habitat-use patterns by both animals and humans.

Fire frequency has probably also decreased at many *E. grandiflorum* sites because of suppression of wildfires and lack of deliberate burning. Landscape burning was widely practiced by plateau aboriginal peoples for a variety of purposes, including maintaining habitat for root vegetable species (Turner 1994). *Erythronium grandiflorum* is well equipped to survive fires because plants become dormant before conditions are warm and dry enough for an area to burn. At many sites it may respond positively to fires because of reduced competition. Fires could also benefit *E. grandiflorum* by preventing tree encroachment, removing litter, and altering soil nutrients.

Distribution of *E. grandiflorum*

Currently, the most extensive suitable habitats for *E. grandiflorum* in western Canada are subalpine meadows, which represent a transition zone between the low light levels of spruce–fir forests and the harsh conditions of alpine tundra. Although most populations of *E. grandiflorum* in western Canada occur in subalpine meadows, plant size and blooming frequency indicate that some low-elevation sites (open meadows or habitats with deciduous shrubs or trees) are more favourable; however, the species is infrequent at low elevations, perhaps because grasslands may often be too dry, whereas most areas with higher moisture levels are forested. We found most low-elevation *E. grandiflorum* sites in transition zones between grassland or dry woodlands and much moister coniferous forests. In these sites, *E. grandiflorum* was often patchy, occupying moist microsites such as small swales that are wet in spring and dry by midsummer. In southwestern Alberta, it occurred under wind-stunted *Populus tremuloides* but did not extend into the drier and more open grasslands. It often occurred under deciduous trees and shrubs, which are still leafless when *E. grandiflorum* flowers.

Erythronium grandiflorum is also infrequent at intermediate elevations in western Canada, probably because of the nearly continuous coniferous forest. We show that *E. grandiflorum* can grow under coniferous canopies but less successfully than in open sites. These treed sites are usually near open areas and may contain "sink" populations of *E. grandiflorum* that persist only because of immigration from nearby, more successful populations. Frequent fires can maintain open areas in otherwise forested landscapes and thus promote the persistence of *E. grandiflorum* populations; landscape burning once performed by native peoples may have been important in this respect. Avalanches can also maintain favourable open habitats.

Erythronium grandiflorum resembles other members of the genus in a number of important respects. All are spring ephemerals, dependent on early season light and moisture (Mathew 1992). They may be important in preventing leaching of nutrients caused by snowmelt (i.e., the "vernal dam hypothesis" put forth by Muller (1978) for *E. americanum*). Some species occur primarily in open areas, as does *E. grandiflorum*, but many are understory plants of deciduous forests where they complete much of their growth before canopy trees leaf out. For example, *E. japonicum* occurs in deciduous, broad-leaf forests of Japan and requires bright light for at least one month in early spring; it declines along a gradient from deciduous to evergreen canopy, where no seedlings or flowering individuals were found (Kawano et al. 1982). However, some species do occur under coniferous canopies; *E. montanum* is a major understory plant in some subalpine, coniferous forests (Antos 1988), although it is also abundant in subalpine meadows (Allen et al. 1996). Thus, *E. grandiflorum* generally resembles other species in the genus, but it stands out in one important respect: its range is much larger than that of any congener in western North America (Applegate 1935; Allen 1993).

The explanation for the large range of *E. grandiflorum* may, in large part, be historical. It is abundant and widespread in subalpine meadows in western North America, and similar habitats were much more extensive after the last deglaciation. Following glacial retreat, cold continental habitats were widespread (Ritchie 1987), which may have allowed rapid spread of *E. grandiflorum* before these subalpine-like habitats became fragmented as the climate warmed. Such a scenario could explain the numerous, currently disjunct populations of *E. grandiflorum*, including those in maritime areas near the coast. Conditions were probably much less suitable for the spread of other western *Erythronium* species, which generally occupy relatively maritime climates west of the Sierra Nevada – Cascade Mountain axis (Applegate 1935; Allen 1993; Allen et al. 1996). Although the very restricted seed dispersal of *E. grandiflorum* (Weiblen and Thomson 1995) might be expected to limit rates of spread, seeds may occasionally move long distances; isolated populations of *E. montanum* appear to result from long-distance dispersal (Allen et al. 1996) and wind movement across snow could have been an effective mechanism of transport (e.g., Matlack 1989; Greene and Johnson 1997) in the extensive open areas following deglaciation. The long and difficult to measure tail of the dispersal curve is critical to interpretation of range expansion and can account for the rapid spread of species, including those with rather restricted dispersal, following the last glaciation (Clark 1998).

Erythronium grandiflorum is not an early successional species (i.e., ruderal sensu Grime 1979), but occurs primarily in permanently open habitats. The species may occur mainly at high elevations in western Canada, not because these represent the most favourable abiotic conditions, but because it is displaced from middle- and low-elevation sites where extensive coniferous forests occur. Such disparity between the fundamental and realized niche may be common for many species that do poorly under forest canopies. If forests in British Columbia were less extensive or composed of deciduous trees, it seems likely that *E. grandiflorum* would be much more abundant. Perhaps at the end of the last glacial period, before trees fully colonized their potential habitat, *E. grandiflorum* had a window of opportunity that can best explain its current widespread distribution with numerous disjunct populations. Such historical periods of reduced species interaction may be pivotal in explaining the distribution patterns of many species that occur on post-glacial terrain.

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