Auteology of Erythronium grandiflorum in western Canada

Dawn C. Loewen, Geraldine A. Allen, and Joseph A. Antos

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 plante 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 associées, et ils ont examiné l’ordonnance 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 1’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 grande 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-equilibrium 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 elaiosomas 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; Cruzen 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° – 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 species 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 bulk 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 were then combined, 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). All sets 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, unredced space (*R* squared 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...
stages and ordination scores. Because most variables were not nor-
mally distributed (as indicated by the Wilk-Shapiro statistic), we
used Kendall’s coefficient of rank correlation, \( \tau \) (McCune and
Mefford 1997). In all, we used 14 environmental and 9
E. grandiflorum quantitative variables for the analyses; some vari-
ables were eliminated prior to analysis because they were highly
correlated with other variables or contained too few non-zero val-
ues to be meaningful (see Loewen 1998 for details of variable se-
lection 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 inter-
preted.

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 de-
ciduous 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, non-
flowering 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 flow-
ering 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 aver-
aged 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 pro-
duced 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 sub-
alpine meadows; this axis showed a strong positive correlation
with elevation (Table 2; Fig. 3a). 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. 3b and 3c). Litter depth and cover
showed significant negative correlations with the first axis (Ta-
ble 2; Fig. 3), indicating higher values for these attributes in
low-elevation grasslands than in subalpine meadows. Two clus-
ters 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
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. 3g and 3h) 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. 3e and 3f). 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.

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

*P < 0.01 (τ = 0.292).
species, 45 showed significant ($P < 0.01$) rank correlations with the first axis and only 13 were significantly correlated with the second axis.

Table 2. Rank correlations (Kendall’s $\tau$) between environmental variables and first and second axis scores of the DCA ordination (Fig. 2) at 38 Erythronium grandiflorum sites.

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

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

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.

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, non-flowering 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. 5a and 6b). 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. 5b and 6d). Both density and proportion of two-leaf, non-flowering plants were strongly correlated with elevation (Fig. 6c and 6e; r = 0.671 and 0.678, respectively), whereas seedling densities were not correlated with elevation (Fig. 5a) or any other measured site factor. Flowering was negatively correlated with conifer abundance (r = -0.673 for proportion of plants flowering and -0.515 for proportion of flowering plants with multiple flowers) (Fig. 6g and 6h), 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. 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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Low elevation Mean</th>
<th>Low elevation SD</th>
<th>High elevation Mean</th>
<th>High elevation SD</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of seedlings (number per metre squared)</td>
<td>8.7</td>
<td>12.4</td>
<td>20.2</td>
<td>16.4</td>
<td>0.0628</td>
</tr>
<tr>
<td>Density of one-leaf plants (number per metre squared)</td>
<td>156.7</td>
<td>62.8</td>
<td>165.3</td>
<td>115.3</td>
<td>0.8282</td>
</tr>
<tr>
<td>Density of two-leaf, non-flowering plants (number per metre squared)</td>
<td>6.2</td>
<td>3.1</td>
<td>26.0</td>
<td>28.9</td>
<td>0.0048</td>
</tr>
<tr>
<td>Density of flowering plants (number per metre squared)</td>
<td>57.0</td>
<td>25.0</td>
<td>27.0</td>
<td>17.1</td>
<td>0.0092</td>
</tr>
<tr>
<td>Proportion of all flowering plants with multiple flowers</td>
<td>0.10</td>
<td>0.09</td>
<td>0.02</td>
<td>0.03</td>
<td>0.0070</td>
</tr>
<tr>
<td>Proportion of all plants (excluding seedlings) that were flowering</td>
<td>0.7</td>
<td>0.11</td>
<td>0.13</td>
<td>0.07</td>
<td>0.0084</td>
</tr>
<tr>
<td>Proportion of two-leaf, non-flowering plants among all plants (excluding seedlings)</td>
<td>0.03</td>
<td>0.02</td>
<td>0.11</td>
<td>0.06</td>
<td>0.0007</td>
</tr>
<tr>
<td>Ratio of seedlings to flowering plants</td>
<td>0.25</td>
<td>0.39</td>
<td>0.76</td>
<td>0.52</td>
<td>0.0070</td>
</tr>
<tr>
<td>Leaf area (cm²)</td>
<td>62.6</td>
<td>26.0</td>
<td>40.5</td>
<td>13.4</td>
<td>0.0170</td>
</tr>
</tbody>
</table>

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

Distribution of *Erythronium grandiflorum*

Currently, the most extensive suitable habitats for *Erythronium 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 *Erythronium 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 *Erythronium 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 subal
pine-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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