



Dispersal limitation inferred from an experimental translocation of *Lomatium* (Apiaceae) species outside their geographic ranges

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Determining limitations on poleward range expansion is important for predicting how climate change will alter the distribution of species. For most species, it is not known what factors set their distributional limits and the role dispersal limitation might play if range-limiting factors were altered. We conducted a transplant study of three related and co-occurring *Lomatium* species at their northern range limits to test competing hypotheses of range limitation. We added seeds to experimental plots inside and outside the species' geographic range (a regional treatment) in a replicated design with vegetation intact and vegetation reduced (a disturbance treatment) and with herbivore access and herbivore exclusion (an herbivory treatment). Germination and reemergence were measured through two growing seasons, along with community-level variables. A fully-crossed linear mixed model revealed that *Lomatium* survivorship outside the current range was as good or better than survivorship within the range, at least when the vegetative community remained intact. This suggests that the species are dispersal limited. Germination often was improved in the presence of an intact vegetative community, but this potentially facilitative effect was absent in second-year reemergence. Plots exposed to herbivory had slightly, but significantly, reduced germination, though reemergence did not differ between herbivore treatments. *Lomatium dissectum*, a rare species, had significantly lower survivorship than its congeners, suggesting that range shifts in rare taxa may be particularly difficult. Seed additions beyond species' range limits may be a strategy for overcoming dispersal limitation and assisting species in poleward migrations.

Changes in climate alter the geographic distributions of many species, presumably because climate limits range expansion (Davis and Shaw 2001, Parmesan and Yohe 2003). If range limits often are set by climate (Woodward 1987), species may expand poleward under regional warming if colonization of newly-suitable sites can be achieved. A wide range of climate-related mechanisms of range limitation have been reported in plants including death from minimum cold temperatures or gradually accumulating sub-optimal weather events and slow pollen tube growth from cool summer temperatures resulting in unfertilized ovaries (Burke et al. 1976, Davison 1977, Pigott and Huntley 1981). Studies on the recent dynamics of species' ranges have observed changes in range boundaries that correlate with climatic changes, suggesting that climate change relaxes climatic limitation (Parmesan and Yohe 2003, Walther 2004). In addition, it is known that species moved to follow postglacial climate changes more often than adapting to new conditions in place (Bradshaw 1991, Davis and Shaw 2001).

It has long been recognized, however, that factors other than climate can limit species' ranges (Griggs 1914, 1940, Prince and Carter 1985), including dispersal limitation, competition and predation. Because habitat near and outside the range boundary of many species is patchy and

fragmented (Gaston 2003), it is possible that dispersal is a predominant factor limiting poleward range expansion, rivaling that of climatic limitation (Matlack 1994, Cain et al. 1998, Grashof-Bokdam and Geertsema 1998, Norton et al. 2005, Svenning and Skov 2005, 2007). Dispersal limitation has been demonstrated at even very local scales of a few meters (Primack and Miao 1992, Eriksson 1998). However, populations successfully colonized habitats over long distances following glaciation, indicating that dispersal is often not completely limiting, at least not over thousands of years when human barriers to migration are absent (Davis and Shaw 2001). Competition also can be an important factor limiting the ecological range of species, and recruitment may be poor for species entering diverse, competitive communities (Elton 1958, Tilman 1997). There is little direct evidence, however, that competition limits the geographic ranges of species (Bullock et al. 2000), though it is often assumed to be an important factor at the equatorial edge of a species' range (Loehle 1998). Soil disturbance has the potential to release resources and reduce competitors, allowing for establishment of newly colonizing species (D'Antonio et al. 1999). Little evidence exists that herbivores limit the geographic ranges of plant species, but herbivory is known to affect the distribution of species at smaller spatial scales (Cantor and Whitham 1989,

Bruehlheide and Scheidel 1999). On one hand, generalist herbivores could limit the establishment of populations outside the historic ranges sometimes as effectively as competitors, by favoring novel food sources (Maron and Vilà 2001, Levine et al. 2004). On the other hand, plant species moving outside their ranges may be released from herbivores in their historic range, allowing for colonization (Maron and Vilà 2001, Keane and Crawley 2002). There is experimental evidence that herbivores sometimes prefer native plant species and other times non-native species (Knapp et al. 2008), but herbivores may facilitate the spread of colonizing species more than they limit their establishment (Maron and Vilà 2001).

Our research examined the range-limiting factors for three *Lomatium* species at their poleward geographic range boundary. This study 1) investigates the potential for range change, 2) determines if related and co-occurring species respond to the same range-limiting factors, and 3) determines species-specific differences in early-life stage survivorship when transplanted to novel locations. Our three study species enable us to address these study objectives in a phylogenetically controlled way. The three species – *Lomatium utriculatum*, *L. nudicaule* and *L. dissectum* var. *dissectum* – belong to the same genus and share important life history traits, including flowering time, dormant season, perennial habit, herbaceous form, insect pollination, and gravity or possibly wind-dispersed seed (Thompson 1985, Douglas et al. 1998, Marsico and Hellmann unpubl.). One obvious difference among them is abundance, a characteristic that may be linked to the ability for geographic range shift (Iverson et al. 2004).

We tested the hypotheses that the *Lomatium* species are climate, dispersal, disturbance, or herbivore limited at the poleward boundary of their geographic ranges. We tested these hypotheses by adding seeds to plots within the current distribution and to seemingly-suitable habitat in areas north of the current maximum northward extent. Equal or better survivorship outside the range would indicate dispersal limitation, as the species would be expected to grow in the outside-range sites if they were able to reach these locations. If survivorship outside the range, however, was less than within the range, the result could be due to abiotic differences between the regions (e.g. climatic differences) or biotic differences. Given similar life histories and genetic relatedness of the species, we hypothesized that range-limiting factors and species' responses to those factors would be qualitatively the same. Underlying differences in abundance among the species, however, suggested that the species could have different baseline germination and reemergence rates.

Our experiment examined climatic factors, vegetation reduction, and ungulate herbivory given their potential importance in new population establishment. It has been suggested that native herbaceous species in the habitats where these *Lomatium* species live are not inferior competitors to non-native taxa, but that they are not adapted to the current disturbance regime and have lower propagule pressure than non-natives (MacDougall et al. 2004, MacDougall and Turkington 2005). Herbivory from Columbian black-tailed deer *Odocoileus hemionus columbianus* also recently has been shown to reduce survivorship of some species in these ecosystems (Gonzales and Arcese

2008). For these reasons, competition and herbivory were included in our experiment.

Other factors such as insect herbivores, mutualists, parasites, pathogens and seed predators also can be important in population establishment and persistence (Thompson 1985, Packer and Clay 2000, Klironomos 2002, Mitchell and Power 2003), but they were not examined in our experiment based on a related study in the literature. Thompson (1998) conducted a long-term study on herbivore and pathogen attack of a population of *L. dissectum* in eastern Washington and found that 36 of 103 individuals were alive after 10 years of monitoring. Of the plants that did not survive, nearly half of the deaths were attributed to pocket gophers feeding on the roots. Other deaths could not be assigned a cause. Additionally, over the ten years of study, each individual was attacked only by a mean of 1.6 above-ground herbivores or pathogens per year out of a total of five common herbivores and pathogens (mammalian herbivores, one moth, two flies and a rust). These results suggest that above-ground herbivory and pathogen attack is a regular event, but it cannot readily be implicated in plant death or lack of establishment. We also expect that plant species are more likely to be released from pathogens outside their native range, rather than negatively impacted by them (Mitchell and Power 2003). It is possible, however, that parasites or diseases could emerge under climate change or over the years following population establishment outside their current ranges.

Methods

Location and study species

We conducted our study on Vancouver Island, British Columbia, Canada, in ecosystems dominated by Garry oak *Quercus garryana* and similar open sites north of the range limit of Garry oak. The climate is sub-Mediterranean, with cool, wet winters and dry summers. North of this region, mean temperatures are cooler and annual precipitation is higher (Results). Species within the Garry oak ecosystem are hypothesized to expand northward within southwestern British Columbia, as warmer temperatures and more extreme seasonal variation in precipitation patterns are expected for the coastal Pacific Northwest (Fuchs 2001, Hamann and Wang 2006). The Garry oak ecosystem is characterized by varying degrees of open oak canopy and a diverse understory of ground flora (MacDougall et al. 2004). Many plants associated with oak savanna of western North America range from California to a northern limit on Vancouver Island. Some typical ground flora associates are found beyond the northernmost oak populations, and these northern herbaceous, open-canopy communities are less invaded by exotic grasses than the Garry oak habitats further south. Large mammalian herbivore communities consist of dense populations of Columbian black-tailed deer *Odocoileus hemionus columbianus* in both regions and elk *Cervus elaphus* in open sites north of the current extent of Garry oak. In many Garry oak habitats, plants are browsed heavily by deer. At the northern limit of Garry oak and its associated flora, habitat patches are typically smaller and

more isolated than patches further south. The three *Lomatium* study species are long-lived perennial herbs that are shade intolerant and grow in association with oak in savanna, rock outcrop or prairie habitats.

Germination trials and seed measurements

As an initial control, we investigated germination rates in a competitor- and predator-free greenhouse environment. Seeds of all three species were collected from five sites for each species on Vancouver Island and brought back to the Univ. of Notre Dame in 2005. Seeds came from 30 *L. utriculatum*, 20 *L. nudicaule* and 21 *L. dissectum* plants and numbered 886, 394 and 447, respectively. Seeds were placed in cold stratification: two weeks for *L. utriculatum*, which germinates earlier than the other two species, and seven weeks for both *L. nudicaule* and *L. dissectum*. Optimum cold stratification times were determined in 2004 for *L. utriculatum* and *L. nudicaule* using purchased nursery seed. *Lomatium dissectum* seed was unavailable for cold stratification trials, but it has a natural germination time similar to *L. nudicaule* so we provided it the same amount of cold stratification. Ten seeds were planted per 6-inch pot with soil with extended release fertilizer (0.09–0.04–0.06). Planted seeds were placed in a greenhouse set at to daily high (15°C) and low (7°C) temperatures representative of long-term average spring conditions in Victoria, British Columbia. Greenhouse lighting was enhanced for 12 hours during day-time hours to represent equinox light conditions. Number of germinants was recorded through 19 weeks. Final germination proportions were tallied for seeds from each mother plant (i.e. 71 values over all three study species) and compared across species using a one-way ANOVA and a Tukey post-hoc comparison. Statistical analysis was performed using Systat 12 (Systat Software Inc., Chicago, IL).

Field experiment

Six planting sites were chosen in spring 2006 to conduct a transplant field experiment. Three sites within the species range were grouped to form the ‘inside-range’ region, and three sites northward of the current range boundary were grouped to form the ‘outside-range’ region (Fig. 1). Sites within a region were separated by at least 4 km, and sites across study regions were separated by at least 186 km. Inside-range sites were located in oak-dominated savanna, with widely spaced canopy trees. Planting plots at these sites were located in full-sun conditions. Suitable open-canopy study sites outside the range of these three taxa are uncommon because of the dense coniferous forest. Therefore, we were limited in the distribution of sites we could select. Two of the three outside-range sites were located on rocky outcrops with naturally no tree canopy. These outcrops ranged in size from one to a few hectares and were bordered by dense coniferous forest. At the third outside-range site, a coniferous forest canopy was cleared by humans and maintained as an open-canopy pasture-like site by mowing. As with plots at inside-range locations, outside-range plots were located in full-sun.

We selected study sites in the outside-range region that have been predicted by climate models to be among the first to become suitable for Garry oak associated species (Hamann and Wang 2006). The outside-range sites are not many kilometers beyond the current northern extent of *L. nudicaule*, but they are sufficient to address the research questions in this study because locations outside the current range by any distance allow for testing the mechanisms involved in range boundary limitation. The outside-range sites were chosen as the most likely to be occupied by shifting species of the Garry oak ecosystem as they are not shaded by coniferous forests and are not separated from the current range by a significant water body. Sites both inside and outside the range have a history of Euro-descendant

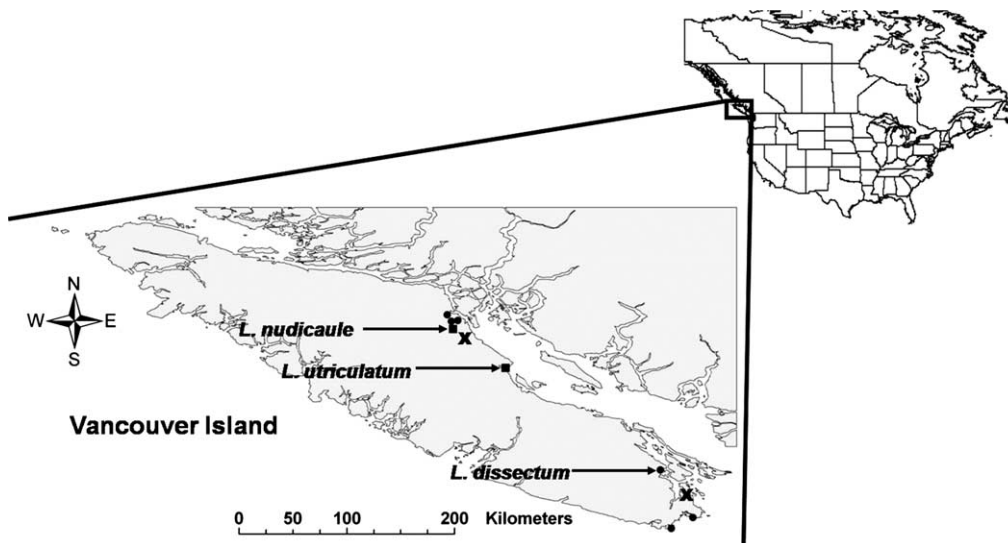


Figure 1. Map of study region on Vancouver Island, British Columbia, Canada, including the six *Lomatium* planting sites (black circles). Three study sites are within the current geographic range boundary of the three *Lomatium* species, and three sites are beyond the northern range limit of all three species. The black squares labeled with species names indicate the most northerly known location of each species. The most northerly within-range planting location coincides with the known northern location of *L. dissectum*. The sites marked with an “X” are the airport weather stations shown in Fig. 5.

land modification including introduction of European native pasture grasses and livestock grazing, but the extent of this use varies between regions and among sites. The three inside-range study sites have a high proportion of introduced herbaceous species, whereas the sites outside the range have been less modified by recent human activity. Fire has been suppressed in both regions. Sites also vary in soil depth with two shallow soil/rock outcrop sites and one deeper soil/pasture-like site in each region.

Twenty 1-m² plots in each of the six sites were stocked with seed: 18 000 seeds of *L. utriculatum*, 10 320 of *L. nudicaule* and 5 520 of *L. dissectum* were collected from four to six sites per species on Vancouver Island. Seeds were attached to toothpicks with non-toxic, water-soluble glue for ease of transport, planting and tracking within the field plots. One hundred and fifty *L. utriculatum*, 86 *L. nudicaule* and 46 *L. dissectum* seeds were placed into each 1-m² plot using the same randomized design (seed placement determined using a random number generator). Seeds were planted at or just below the soil surface under a 1-m² grid of plastic mesh (deer fence) staked to the ground. The deer fence grid was comprised of 900 6.25-cm² cells, 282 of which were planted with seeds.

Each 1-m² plot was treated with one of two levels of a disturbance (vegetation reduced and vegetation intact) and an herbivory (herbivores excluded and open to herbivores) treatment. Treatments were randomly assigned to the plots such that one quarter were controls, one quarter were given a vegetation reduction treatment, one quarter were given a herbivore exclusion treatment, and one quarter had vegetation reduced and herbivores excluded. Each treatment combination was replicated five times at each site.

We reduced vascular plant species richness and biomass in vegetation reduction (VR) plots by hand-pulling plants and digging out roots, rhizomes and bulbs near the soil surface before seed planting. This VR treatment was a pulse experimental treatment, as it was only applied once before seed additions. To avoid dramatic soil temperature differences due to dark colored soil and the potential for wind or water erosion in VR plots, the VR plots were covered with a thin layer of removed plant material. Mechanical VR has the combined effect of reducing vegetation that can have a facilitative or competitive influence on the *Lomatium* plants and disturbing the soil, which can free previously unavailable resources (Discussion). The other half of the plots received no manipulation, which provided natural vegetation conditions and undisturbed soil. The herbivore exclusion (HE) plots were covered with deer fence supported by a PVC cage (1 × 1 × 0.5 m) to limit access by herbivores. We focused on excluding large mammalian herbivores. In addition, our cage design also had the effect of excluding egg-laying females of the anise swallowtail butterfly *Papilio zelicaon*, an insect herbivore of the *Lomatium* species (Marsico and Hellmann unpubl.). Cages were kept over the plots for the entire study period, constituting a press experimental treatment.

Lomatium seeds were planted in July 2006. Germination was assessed in April 2007. When ungerminated seeds were readily found, they were recorded so that the fate of as many seeds as possible was known. Reemergence was assessed in April 2008. The proportion of germination was calculated for each species in each plot by dividing the number of

living individuals by the number of seeds planted. The proportion reemergence was calculated by dividing the number of living individuals by the number that had germinated the previous year.

Field experiment statistical analyses

Lomatium species, region, vegetation and herbivory treatments applied to the plots were used as main effects in a linear mixed model to determine the influence of the applied treatments on *Lomatium* establishment. Proportion germinated (i.e. survivorship from seed) was the response variable in 2007, and proportion reemerged (i.e. survivorship since germination) was used in 2008. Because factors promoting or inhibiting seed germination can differ from factors involved in plant reemergence, the linear analysis was conducted separately for germination and reemergence. The linear mixed model was a fully crossed design of fixed effects (species, region, vegetation and herbivory). This model also included site and plot as random effects. Plots were replicated within sites and each contained all three study species. Therefore, any influence on the survivorship responses associated with a plot effect was accounted for as a random effect in the mixed model. Likewise, unmeasured variables associated with each of the three sites within region may have influenced survivorship of the *Lomatium* plants, so site was included as a random effect. Testing the linear mixed model assumptions of normally-distributed and homoscedastic errors was conducted by visualizing the plotted residuals. Germination data met the assumptions, and reemergence data showed only slight departures from normality and homoscedasticity. For studies having similar sample sizes to this one, the linear mixed model has been shown to be robust for inference on fixed effects even when the model assumptions are not met (Jacqmin-Gadda et al. 2007). Therefore, we did not transform the reemergence data. Statistical analysis was performed using SPSS 16 (SPSS Inc.).

Environmental measurements and analyses

Light is likely an important limiting resource in the establishment of native plants in the Garry oak ecosystem (MacDougall and Turkington 2007). The amount of light reaching the plots was determined for all plots at two sites, one within-range (April 2007) and one outside-range (May 2007), with a quantum meter. Light measurements from one site within each region were adequate for the analysis because plant height and coverage were similar among sites within region (data not shown). Light levels reaching the soil surface at these sites also were calculated, and the difference between light reaching the plot and light reaching the ground was analyzed in a two-factor ANOVA ('ltANOVA') that included site and vegetation treatment as main effects. The ltANOVA was conducted using Systat 12. Assumptions of normality and homogeneity were met.

Soil moisture data were collected to 1) assess the change in soil moisture over the growing season, 2) determine if experimental treatments had an impact on soil moisture, and 3) determine if site-level *Lomatium* survivorship was related to soil moisture. Soil moisture was determined with

a Hydrosense TDR using 12 cm probes at four points within each plot in April, May and June 2007. The four plot-level readings were averaged to obtain a plot-level measurement. Pearson correlations of soil moisture were conducted between each pair of months sampled (April/May, May/June, April/June) to determine the consistency among plots in soil drying over the growing season. We conducted a three-factor ANOVA on June moisture ('smANOVA'), the driest month sampled. Region, vegetation and herbivore treatments were included as factors in the model to determine if the treatments imposed on the plots impacted soil moisture. In addition, a one-way ANOVA with site as the factor was conducted on June soil moisture, and a Tukey post-hoc comparison was conducted to determine pairwise differences between sites. We then used least squares linear regression to relate site-level mean 2008 survivorship for each species with site-level mean June soil moisture levels. These regressions were used to determine if there was a significant relationship between soil moisture at the end of the first growing season with survivorship in the second growing season.

Finally, we determined if climatic conditions outside the current *Lomatium* distribution are historically or recently similar to conditions inside the range (i.e. a comparison of climate envelopes). We obtained climate data for 26 known *Lomatium* sites in British Columbia and northern Washington and for the three outside-range planting sites using ClimateBC ver. 3.2 (Wang et al. 2008). ClimateBC is a program that extracts and downscales PRISM (Daly et al. 2002) data to calculate site-specific climate estimations. Climate data from 1960–1990 were used for recent climate, and data from 1901–1930 were used for site-level climate estimation further in the past. Ten annual climate variables (mean annual temperature, mean warmest month temperature, mean coldest month temperature, mean annual precipitation, mean annual summer precipitation, degree-days below 0°C, degree-days above 5°C, Julian date for beginning of frost-free period, mean annual snowfall and extreme minimum temperature) and three mean monthly variables (maximum mean temperature, minimum mean temperature, and precipitation) were used to simplify these site-level climate estimates into two principal component axes (PC1 and PC2) using SPSS 16. Factor scores for PC1 and PC2 were plotted for all 29 locations, and the value for the PC scores for the outside-range sites were compared to the sites within the range.

In addition, to capture directional change in climate inside and outside the range and to determine if conditions during the experiment were typical for the region, we gathered annual and monthly climate data from the Environment Canada National Climate Archive (<www.climate.weatheroffice.ec.gc.ca/>) for the Victoria International (YYJ) and Campbell River (YBL) Airports during 1965–2006 (annual climate data), 1971–2000 (monthly climate data), and July 2006–April 2008 (monthly weather data during experiment) (Fig. 1). YYJ is located between the southern and northern within-range sites (within 40 km), and YBL is near the three sites outside the range (within 20 km) (Fig. 1). Mean annual temperature, total annual precipitation, annual snowfall and annual extreme minimum temperature were regressed against time to examine recent climatic change. We used available monthly weather

data (monthly mean temperature, monthly mean maximum temperature, monthly mean minimum temperature, monthly extreme maximum temperature, monthly extreme minimum temperature, total monthly precipitation and total monthly snowfall) to determine how weather variables during the experiment related to long-term averages.

Results

Germination trials and seed measurements

In the greenhouse, the first flush of germination happened within two weeks of planting for all three species, and within four weeks, all *Lomatium dissectum* germination was complete. Proportion of seeds germinated after 19 weeks averaged 0.61 (SE = 0.03) for *L. utriculatum*, 0.39 (SE = 0.06) for *L. nudicaule* and 0.03 (SE = 0.02) for *L. dissectum*. ANOVA results and Tukey post-hoc comparisons show that germination rates were significantly different among species ($F_{2,68} = 58.6$, $p < 0.001$).

Field experiment

From the linear mixed model we determined that the factors important in germination success were largely the same as those important in reemergence. The interaction between species, region, and the vegetation treatments was significant during germination and nearly so for reemergence (Table 1). All two-way interactions between species, region, and vegetation were significant in both years (Table 1, Fig. 2). It is important to note, however, that region as a main effect was not significant in either germination or reemergence, indicating that sites outside the range are conducive to *Lomatium* growth (Table 1). In addition, though region is a factor in two significant interactions (species \times region and region \times vegetation), survivorship was not reduced outside the range relative to within the range for any of the species when the vegetation in the plots remained intact (Fig. 2). None of the species showed reduced reemergence from the VR treatment. For the most part, the region \times vegetation interaction is driven by the fact that survivorship was not reduced outside the range in vegetation-intact plots, but survivorship outside the range was lower than inside the range in VR plots. Species identity as a main effect was important in determining survivorship success during both years (Table 1, Fig. 2). *Lomatium dissectum*, the rarest species, had lower germination and reemergence than the other species. It is likely that any interaction among the planted *Lomatium* individuals was small due to their spacing in the plots and small size.

Environmental measurements

The amount of light intercepted by the vegetation was $389 \mu\text{mol m}^{-2} \text{s}^{-1} \pm 60 \text{ SE}$ for the VR plots at the outside-range site, $499 \pm 61 \text{ SE}$ for intact vegetation plots at the outside-range site, $397 \pm 59 \text{ SE}$ for VR plots at the inside-range site, and $825 \pm 103 \text{ SE}$ for intact vegetation plots at the inside-range site. Lower values indicate that more light was reaching the soil surface. The two-factor ltANOVA

Table 1. Covariance parameter estimates for random effects and F-ratio tests for fixed effects of the fully crossed linear mixed model for *Lomatium* species germination (2007) and reemergence (2008). Bold font p-values are significant at $p < 0.05$. Denominator degrees of freedom for 2008 differ from those in 2007 due to missing values.

Random effect	Germination (2007)				Reemergence (2008)		
	Covariance parameter estimates				Covariance parameter estimates		
Site			0.0015			0.0608	
Plot			0.0050			0.0109	
Fixed effect	Numerator DF	Denominator DF	F-ratio	p-values	Denominator DF	F-ratio	p-values
Species (S)	2	224	67.72	< 0.001	218	60.09	< 0.001
Region (R)	1	4	0.72	0.445	4	0.01	0.920
Vegetation (V)	1	108	13.46	< 0.001	107	0.52	0.474
Herbivory (H)	1	108	4.59	0.034	107	0.17	0.679
S × R	2	224	6.53	0.002	218	19.12	< 0.001
S × V	2	224	25.64	< 0.001	218	3.79	0.024
S × H	2	224	0.52	0.595	218	0.26	0.772
R × V	1	108	18.00	< 0.001	107	7.05	0.009
R × H	1	108	0.00	0.990	107	0.18	0.672
V × H	1	108	3.19	0.077	107	2.61	0.109
S × R × V	2	224	4.29	0.015	218	2.16	0.117
S × R × H	2	224	0.27	0.764	218	1.70	0.185
S × V × H	2	224	0.09	0.918	218	0.32	0.728
R × V × H	1	108	0.01	0.909	107	0.03	0.864
S × R × V × H	2	224	0.54	0.586	218	0.81	0.446

showed a significant interaction between site and vegetation treatment ($F_{1,36} = 4.76$, $p = 0.036$) because even though the VR plots had a reduced amount of intercepted light (treatment main effect, $F_{1,36} = 13.57$, $p = 0.001$), the reduction was greater for the inside-range site because the intact vegetation was denser and taller (site main effect, $F_{1,36} = 5.27$, $p = 0.028$; density and height data not shown).

Progressive soil drying was observed at all sites from April through June. Pearson correlations for monthly soil data showed that plot-level soil moisture values in April were highly positively correlated with values in both May ($r = 0.947$) and June ($r = 0.830$). May, likewise, was highly correlated with June values ($r = 0.825$). The smANOVA showed that region had a significant effect on soil moisture

($p < 0.001$), but vegetation removal ($p = 0.446$) and herbivore exclusion ($p = 0.388$) did not and neither did any interaction. Soils had a higher water content outside the range than inside the range, an outcome driven by two of the three sites (Fig. 3). For *L. utriculatum* and *L. dissectum*, higher levels of soil moisture trended toward lower survivorship, but the relationships were not statistically significant (*L. utriculatum*: $n = 6$, $R^2 = 0.24$, $p = 0.18$; *L. nudicaule*: $n = 6$, $R^2 = 0.00$, $p = 0.50$, *L. dissectum*: $n = 6$, $R^2 = 0.14$, $p = 0.25$).

Principal components analysis of estimated site-level climate data resulted in an explanation of 83.7% of the total variance within the first two principal components for 1901–1930 climate data (PC1 explained 69.9% and PC2 explained 13.8%) and 85.8% for 1961–1990 data (PC1

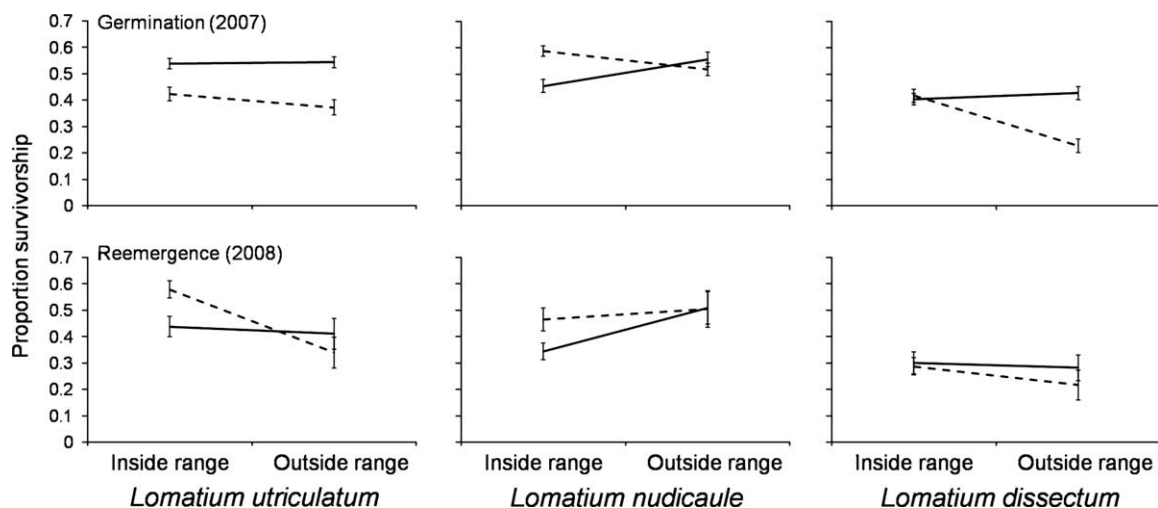


Figure 2. Germination (2007) and reemergence (2008) for each species under the region and vegetation treatments. Solid lines are vegetation-intact treatments, and dashed lines are vegetation-reduction treatments. Error bars are SE.

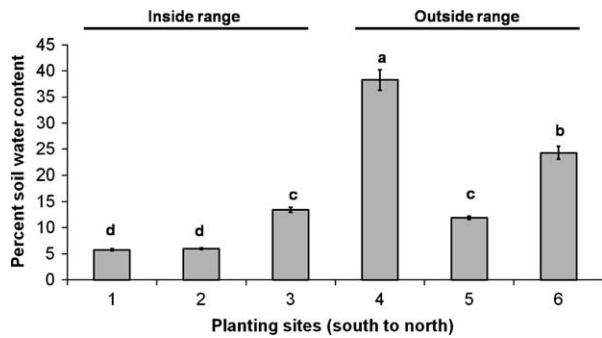


Figure 3. June 2007 soil moisture by *Lomatium* planting site. Sites are displayed from south to north, such that the left three sites are within-range locales and the right three sites are outside-range sites. Error bars are standard error. Different letters above bars indicate significant differences at $p < 0.05$.

explained 72.6% and PC2 explained 13.2%). For both climate periods, most of the 46 climate variables used in the analysis were loaded on PC1. Nine variables related to summer temperature, however, were loaded on PC2. For the early 20th century climate data, sites outside the range boundary had climate estimates within the span of values for locations that support *L. utriculatum* and *L. nudicaule* populations, though conditions in these outside-range sites were toward the low end of PC1 (Fig. 4a). The late 20th

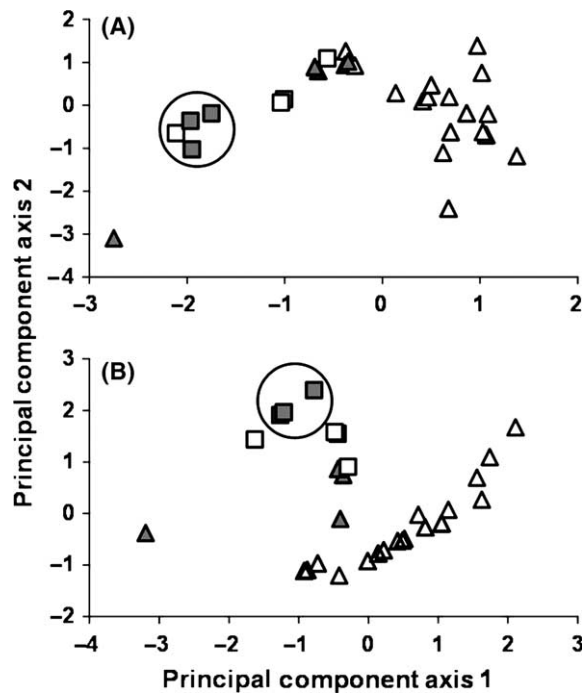


Figure 4. Principal components factor scores for estimated site-level climates for 26 naturally occurring *Lomatium* sites and the three outside-range planting sites for the climate periods (A) 1901–1930 and (B) 1961–1990. Open triangles are locations within the latitudinal range of all three *Lomatium* species; filled triangles are locations within the latitudinal range of *L. utriculatum* and *L. nudicaule*; open squares are locations within the latitudinal range of *L. nudicaule* only; and filled squares are planted outside-range sites (refer to Fig. 1). In both panels, outside-range sites are circled to easily compare the positions of these sites relative to the other *Lomatium* locations.

century climate data revealed a shift in these outside-range sites, such that they still were on the low end of PC1 (though less so than earlier in the century), but they were the three highest sites on PC2 (Fig. 4b).

Linear regressions of climatic change at YYJ (inside-range) and YBL (outside-range) showed an increase in mean annual temperature at both locales from 1965 through 2006 (YYJ $R^2 = 0.481$, $F_{1,40} = 38.9$, $p < 0.001$; YBL $R^2 = 0.413$, $F_{1,38} = 28.4$, $p < 0.001$; Fig. 5). Using the regression line as a mean value, the annual mean temperature in 2006 at YBL is equivalent to the annual mean temperature at YYJ in 1976 (Fig. 5). Extreme minimum temperature has not significantly changed at YYJ, but it has increased significantly in recent years at YBL, though variability is high and is not well predicted by year ($R^2 = 0.082$, $F_{1,38} = 4.5$, $p = 0.041$). Minimum temperatures in any given year between the two locations are always colder at YBL, though across years there is substantial overlap in minimum temperature. Snowfall has seen no consistent change at YYJ, but it has decreased at YBL ($R^2 = 0.120$, $F_{1,39} = 6.5$, $p = 0.015$). Accumulated annual precipitation shows no pattern with time at either location over the last 41 years and is higher at YBL than at YYJ (1454 vs 880 mm on average per year).

Throughout the duration of the experiment (July 2006–April 2008), monthly weather variables at YYJ and YBL only deviated from long-term climatic averages (1971–2000) a few times. At both YBL and YYJ, July and August 2006, were warmer than the long-term average, and July 2007 was warmer at YYJ (data not available for YBL). YYJ recorded a record high temperature in July 2007 of 36.3°C. Mean monthly minimum temperatures were at or above the climatic average except for January 2007, and November 2007, through April 2008, at YYJ. During the course of the experiment, monthly extreme minimum temperatures remained well above the all time coldest values in the climate record for either location. November 2006 was cooler than the climatic average at YBL, and for both YBL and YYJ recorded rainfall was 1.5 and 2.2 times the long-term average. Additionally, that month there was 6 and 12 times the average snowfall at YBL and YYJ, respectively. Both locations received more precipitation than average during the winter of 2006–2007. We conclude that weather was within the range of normal climatic conditions since 1965 in both study regions.

Discussion

For all three species, field plots with the vegetation community intact outside the geographic range had equal or better survivorship when compared to plots within the current distribution. This is more consistent with the hypothesis of dispersal limitation for each of the study species than it is for climatic limitation. This study also suggests that the intact community of shade-intolerant, herbaceous plants northward of the current range of Garry oak associated species can be invaded, and seed additions can overcome dispersal limitation.

Our data indicate that the climate of the outside-range sites has recently changed but conditions have been within the climate envelope of *Lomatium* for at least 100 years. Therefore, our data do not support the hypothesis that

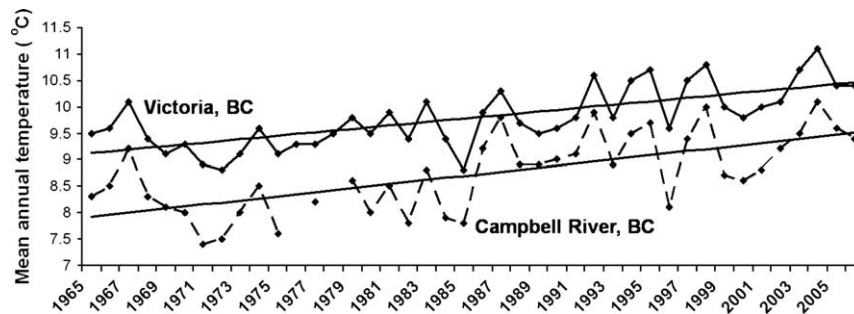


Figure 5. Trends in annual mean temperature in Victoria (YY) and Campbell River (YBL), British Columbia, from 1965 through 2006. $R^2=0.48$ for YY and 0.41 for YBL.

recent climatic changes have made the outside-range sites more suitable, though we do show evidence for changing conditions within the last 50 years. It is possible that inadequate long-distance dispersal may be determining the current poleward range limit of these *Lomatium* species because they may have never realized their full fundamental climatic niche following their migrations onto Vancouver Island after the Last Glacial Maximum. If this is the case, habitat that has long-been suitable for population establishment has remained uncolonized. This scenario is likely because suitable habitat patches north of the current range are small and isolated. Though our data cannot directly address the hypothesis of postglacial dispersal limitation, maternally-inherited chloroplast genetic markers in *L. utriculatum* show limited colonization from mainland sources to the glaciated peripheral range, largely on Vancouver Island (Marsico and Hellmann unpubl.).

Vegetation reduction did not confer an advantage to any of the three species outside the range, possibly because competition for resources outside the range is less intense than within the range. Within the range, *L. nudicaule* benefited in both years from having vegetation reduced, potentially because interactions with neighboring plants are negative throughout the early life stages of *L. nudicaule*. For *L. utriculatum* and *L. dissectum* in the first year, we found a negative impact from the VR plots relative to the vegetation-intact plots. This may mean that vegetation removal has a direct negative effect (e.g. through soil disturbance) on germination, or it is possible that vegetation removal reduces a positive, facilitative impact from an intact vegetative community. Though it is possible that these two *Lomatium* species were negatively responding to an element of the soil disturbance caused from the VR, this would be a unique response for a germinating species because other research generally shows positive responses of germination to soil disturbance (Isselstein et al. 2002, Hierro et al. 2006).

Recently, it has been recognized that facilitation is widespread and important, particularly in environments toward the edge of a species' tolerances (Choler et al. 2001, Callaway et al. 2002, Bruno et al. 2003, Brooker et al. 2008). The mechanisms of facilitation include buffering individuals from herbivores or environmental extremes. Because *L. dissectum* germinated significantly less under the treatment combination of outside-range and VR (i.e. the treatment combination with the lowest coverage of vegetation; data not shown), facilitation from the surrounding vegetation seems to be a fitting explanation for the observed germination patterns in this species. If the VR treatment itself negatively

impacted germination, we would expect to see reduced germination in VR plots in both regions. In fact, we observed that response in *L. utriculatum*, but because of additional evidence, we hesitate to dismiss facilitation as important to *L. utriculatum* germination. *Lomatium utriculatum* germinated earlier than other members of the community germinated or reemerged. Standing biomass from the previous year might have been able to buffer *L. utriculatum* seedlings in vegetation-intact plots in both regions, but facilitative influences would not be possible at the time of *L. utriculatum* germination in the VR plots at the within-range sites, even though these sites later in the season had greater vascular plant coverage, plant height, and species richness than either vegetation treatment in outside-range sites (Marsico 2008). For both *L. utriculatum* and *L. dissectum*, any facilitation effect provided by the vegetative community during germination was reduced upon reemergence. We hypothesize that there is a transition from facilitation during germination toward competition in later growth.

Even though deer herbivory recently has been shown to be exceedingly important to some species in the Garry oak ecosystem (Gonzales and Arcese 2008), it does not seem to have an effect on *Lomatium* establishment. Germination was slightly, but significantly, higher where herbivores were excluded, but this main effect was no longer significant upon reemergence. In addition, the presence of elk within the sites outside the current *Lomatium* species range did not differentially impact *Lomatium* survivorship at those locales.

In both the greenhouse and field experiment, our data suggest that the rare species, *L. dissectum*, has the lowest germination and reemergence. Thus, for management projects such as habitat restoration, our results indicate that more seeds are required from *L. dissectum* than the other two species to obtain the same number of seedlings. This may be difficult due to the low number of seed producing plants on Vancouver Island. Constraints on reproductive output are generally the rule for rare species (Gaston and Kunin 1997, Murray et al. 2002). In contrast, lower germination and survivorship of rare taxa, as found here, is equivocal.

A number of caveats are important to consider regarding this experiment. One factor not explicitly accounted for is the impact of small mammals, including seed predators and root herbivores, and insect seed predators. Studying *L. dissectum* in eastern Washington, Thompson (1985) found that after 10 months (July to May), ~10% of seeds set out in piles remained, only 0.76% germinated, and all of those plants died within two months. Two years later, when populations of seed predators were higher, more than 95%

of seeds were eaten within four months. Our levels of seed predation are far lower, as seen from the high germination success. Further, for both *L. nudicaule* and *L. dissectum*, germination in the field was higher than that observed in the predator-free greenhouse environment. Lastly, we occasionally found intact, ungerminated seeds during our germination assessment, providing evidence that even some of the seeds that failed to germinate remained in the plots uneaten. We also observed some plots at a few sites with active tunneling by voles (*Microtus*). Vole activity, tunneling and root-feeding, has the potential to significantly damage the large taproot of the *Lomatium* species, but in this study only very few plants were affected by root damage because of their small size. As plants grow, however, root-damaging mammals may have an increased impact on survivorship at sites within the range where these mammals were observed.

We did not measure reproductive output in this experiment because the *Lomatium* species did not reproduce during the course of the study. Tracking survivorship through reproduction is important to capture fitness differences among the study regions and experimental treatments because plants can grow and survive in regions where reproduction is not successful (Pigott and Huntley 1981). Survival to reproduction also is critical to population persistence without relying on inputs of seed from outside sources. Nevertheless, understanding early survivorship outside the range relative to within the range is important for long-lived perennials irrespective of reproductive ability because if conditions are not currently suitable for successful reproduction outside the range, established plants can grow and store resources until conditions become suitable. Also, if conditions for reproduction are met in only some years outside the range, this would favor the successful colonization of iteroparous, long-lived perennials such as the species used in this study (as opposed to annual species; Norton et al. 2005).

It is likely that herbivore and competitive communities will be altered under climate change, which may alter the ability of species to establish, particularly in new areas outside their historic ranges. Under current conditions, however, we find that even fragmented habitat beyond the range margin is suitable for colonization of *Lomatium*, given seed additions that overcome dispersal limitation. Interestingly, this study shows that *Lomatium* survivorship is similar between the two regions, though each region has different assemblages of plant and herbivore species.

It is important to understand the factors involved in range limitation to determine the need for management strategies such as assisted migration (also called managed relocation) and to gather appropriate information necessary to implement such conservation measures (McLachlan et al. 2007, Hoegh-Guldberg et al. 2008, Richardson et al. 2009). Our data show successful establishment given seed additions in both intact and VR plots beyond the current species range, indicating that these species may be able to successfully establish new populations given enough propagule pressure. This study provides evidence that an assisted migration strategy may be viable for species that are dispersal limited, and protected areas outside the historical distribution of target species could be used for establishment. Seed additions alone may be relatively inexpensive. Assistance in moving species poleward may be important in establishing local seed source populations in new areas early, allowing for

more short-distance dispersal events to take place if the vegetation structure changes due to climate change (Hebda 1997). Experimental populations would have to be monitored after seed additions to determine if growth and survivorship of the planted individuals results in a reproductive, self-sustaining population.

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