



## **Effects of Snowmelt Timing and Neighbor Density on the Altitudinal Distribution of *Potentilla diversifolia* in Western Colorado, U.S.A**

Author: Stinson, Kristina A.

Source: Arctic, Antarctic, and Alpine Research, 37(3) : 379-386

Published By: Institute of Arctic and Alpine Research (INSTAAR),  
University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2005\)037\[0379:EOSTAN\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2005)037[0379:EOSTAN]2.0.CO;2)

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Effects of Snowmelt Timing and Neighbor Density on the Altitudinal Distribution of *Potentilla diversifolia* in Western Colorado, U.S.A.

Kristina A. Stinson

Ecology and Evolutionary Biology,  
Princeton University, Princeton, NJ 08544,  
U.S.A., and Rocky Mountain Biological  
Laboratory, Gothic, CO 81224, U.S.A.  
Present address: Harvard University,  
Harvard Forest, P.O. Box 68,  
Petersham, MA 01366, U.S.A.  
kstinson@oeb.harvard.edu.

## Abstract

Range limits of temperate high-altitude plants may be controlled by tradeoffs between physically severe but uncrowded conditions, versus mild but crowded conditions. Because up-slope migration of lowland species may accompany global warming and earlier snowmelt, I tested whether crowding by neighbors vs. timing of snowmelt limit *Potentilla diversifolia* to later-melting sites in the Rocky Mountains (U.S.A.). I transplanted individuals from two altitudes to experimental plots within and below the species' range limit, and experimentally altered snowmelt timing and the density of neighboring vegetation. In contrast to theoretical predictions for biotic control of lower range limits, higher temperatures and drier soils contributed to markedly reduced survivorship and reproduction below the native-range regardless of treatment. Neighbor removal only marginally increased performance both within and below the native-range, suggesting that interactions with neighboring vegetation are much less important for distribution than abiotic factors. Populations from the subalpine zone had longer growth intervals and grew larger than those from the alpine tundra in their native sites, but did not outperform alpine tundra populations when grown below the species' range. Although earlier snowmelt enhances growth, phenotypic plasticity may enable *P. diversifolia* to persist in later-melting tundra sites while higher temperatures and drought restrict it from much of the subalpine zone.

## Introduction

One of the central objectives of plant population ecologists is the explanation of species' range limits. The classical literature asserts that abiotic factors control species' distributions toward more stressful ends of environmental gradients, while increasing biotic pressures control distribution as abiotic conditions become milder (Connell, 1961; Holderidge, 1967; MacArthur, 1972). In vascular plant species, upper altitudinal and latitudinal range limits are typically attributed to density-independent mortality caused by abiotic factors such as low temperature and short growing seasons, whereas lower range limits are generally ascribed to biotic constraints such as competition, herbivory, and disease (e.g., Dahl, 1951; Daubenmire, 1954; Billings and Bliss, 1959; Tranquillini, 1964; Woodward and Williams, 1987; Hoffman and Blows, 1994; Heegaard, 2002). A common explanation for this prediction is that adaptations to harsh abiotic environmental conditions will result in more conservative resource use and subsequently lower competitiveness (Grace, 1987), leading to tradeoffs between stress tolerance and competitive ability of a species (Grime, 1979).

Very few empirical studies have tested the relative roles of biotic and abiotic factors on high-altitude plant distribution. In temperate mountains, two major factors that differ widely along altitudinal gradients are the timing of snowmelt and density of vegetation cover. Altitudinal zonation of alpine and subalpine plant species is frequently explained by the idea that there are inherent tradeoffs between persisting in the relatively warm, sheltered, and crowded environments of the subalpine zone, versus the physically severe, open habitat of the alpine tundra (Dahl, 1951; Box, 1995; Pauli et al., 1999; Heegaard, 2002). Subalpine habitats are typically earlier-melting than alpine sites, although steep slopes and wind exposure can result in earlier snowmelt in many alpine sites. Microtopographical variation also lends to local

heterogeneity in species distributions, timing of snowmelt, vegetation density, nutrient availability, soil moisture, and edaphic properties within the alpine and subalpine zones (Billings and Bliss, 1959; Walker et al., 1993; Stanton et al., 1994). Nevertheless, snowmelt timing, vegetation cover, and species' distributions are commonly correlated along altitudinal and local snowmelt gradients (see Billings and Bliss, 1959; Walker et al., 1993; Körner, 1999). Vegetation density generally declines with increasing elevation (Kudo and Ito, 1992; Heegaard, 2002), and many studies have confirmed early classical demonstrations of inter- and intraspecific declines in growth rates and plant size from low to high altitude (e.g., Körner, 1999). Although strong correlations suggest causal links between snowmelt timing, vegetation cover, and distribution, direct tests are needed to identify which factors are most important in maintaining subalpine and alpine plant species' range limits. Moreover, although ecotypic variation across altitudes is common (Turesson, 1922; Clausen et al., 1948; Gurevitch, 1992; Stanton et al., 1997), few studies account for potential differences in the relative response of populations at high and low altitudes to biotic and abiotic factors (Galen, 1990). Because anthropogenically altered temperature and precipitation are expected to affect the distribution and performance of high-altitude plants (Grabherr et al., 1994; Körner, 1999; Walker et al., 1999), species and population-level studies that experimentally decouple biotic and abiotic factors related to early and late snowmelt can be useful for predicting potential migrations, range expansion, or local extinctions in response to global climatic change.

This study investigated the effects of snowmelt timing and neighbor density on the performance of a high-altitude cinquefoil, *Potentilla diversifolia* Lehm. (Rosaceae) in the western Rocky Mountains of Colorado, U.S.A. *P. diversifolia* is most abundant in

moist alpine tundra habitat, though it also occurs in locally later-melting sites at the upper subalpine boundary, and occasionally in very late-melting portions of the middle and lower subalpine zone (Weber and Wittmann, 1996). The alpine sites inhabited by *P. diversifolia* typically have lower vegetative cover but experience up to 30 days later snowmelt than the subalpine meadows (Stinson, 1998). Later-melting alpine sites are also characterized by other abiotic stresses such as low temperatures and short growing seasons that can vary over remarkably short distances (e.g., Billings and Bliss, 1959; Bliss, 1985; Stanton et al., 1997). This species' small stature, slow growth rate, and rapid reproductive phenology fit Grime's description of stress-tolerance traits and are likely to be disadvantageous in more crowded, earlier-melting zones despite the potential benefit of a longer growing season (Bliss, 1962).

In order to test the relative importance of the predominant abiotic and biotic factors in restricting *P. diversifolia* to later melting sites, I experimentally altered neighbor density and snowmelt timing within and below the species' current range. I predicted that higher neighbor densities, rather than earlier snowmelt, would explain the general absence of *P. diversifolia* from the subalpine zone. Because *P. diversifolia* experiences earlier snowmelt and increasing cover of neighboring vegetation in lower altitude sites, it is possible that populations at low and high altitudes demonstrate ecotypic variation in their responses to increasing levels of above-ground competition or abiotic stress (Jurjavic et al., 2002). Therefore, I also tested whether populations growing at lower altitudes responded differently to the transplanting, snowmelt, and neighbor removal treatments than populations originating on the alpine tundra.

## Materials and Methods

### ALPINE TRANSPLANT

In the first experiment, three typical alpine populations of *P. diversifolia* were reciprocally transplanted into their native habitat (approximately 3750 m elevation) and into a sub-alpine meadow located well below the species' natural range (approximately 2750 m) at study sites in Gunnison National Forest, western Colorado. This "alpine transplant" experiment focused on *P. diversifolia* populations in the most common habitat. In the alpine zone, this species co-dominates with other sparsely distributed herbaceous perennials such as *Rydbergia grandiflora*, *Trifolium parryi*, mixed graminoid species and interspersed low-lying *Salix* species. The subalpine meadow site sits below the species' range limit and emerges from snowmelt up to one month earlier than the alpine tundra. This mixed perennial community includes *Potentilla pulcherrima*, *Delphinium nuttallianum*, *Frasera speciosa*, *Ipomopsis aggregata*, and *Trifolium parryi*, along with occasional shrubs and graminoids (Weber and Wittmann, 1996).

A total of 648 adult *P. diversifolia* individuals with a standard rooting depth (7.5–10 cm) and early season rosette diameter (5–7.5 cm), were excavated from native sites in August 1995. Individuals were evenly divided for immediate transplanting into one of three replicate 12 m × 9 m transplant plots below their native-range, and three similar gardens within the native-range. Thirty-six individuals from each population were randomly assigned to positions, ~50 cm apart, in each garden (3 populations × 36 individuals = 108 transplants per garden; 108 transplants × 3 gardens × 2 transplant locations = 648 plants). Transplanting was accomplished with a small hand trowel, using care not to disturb the surrounding vegetation in the transplant gardens. Plots were marked with 4-m stakes for identification prior to snowmelt in the following growing seasons.

A snowmelt treatment and a neighbor removal treatment were implemented in the three replicate gardens at each transplant location in May–June of 1996 and 1997. Snowmelt was delayed by an average

of 15–20 days on one-third of each garden, by securing reflective tarps over a randomly selected 3 m × 12 m subsection of each plot. Another subsection of each plot was subjected to removal of neighboring plants, to mimic the low above-ground vegetation cover in typical alpine sites. The neighbor removal treatment was implemented by clipping entire above-ground parts of all plants within a 50 cm radius of each experimental individual throughout the growing season, thereby minimizing interactions with neighbors. This treatment did not alter snowmelt timing, but reduced natural plant densities equally in both the subalpine and alpine gardens. The final third of each plot was unmanipulated.

Plant performance was monitored during the growing seasons of 1996 and 1997. In both years, data from weekly censuses were used to obtain maximum leaf area (cm<sup>2</sup>) and active growth interval (number of days from emergence to senescence). An estimator for leaf area was developed from the formula for area of an ellipse = (0.50 rosette length × 0.50 rosette width) regressed against a subsample of actual total plant leaf area ( $R^2 = 0.97$ ). Survival and reproduction were measured by counting the number of plants that had survived and/or produced any reproductive parts (buds, flowers, and fruits) by the end of the experimental period. Previous results have shown that this estimate of fecundity is highly correlated with total number of fruits, fruit biomass, and germination rate in this species (Stinson, 1998).

Treatments were subdivided into four quadrants for environmental measurements. The average date of snowmelt for each treatment per plot was derived from the dates of bare-ground appearance within each quadrant. Soil temperature and soil moisture in each quadrant were measured weekly. Soil thermometers were installed at each center point of each quadrant (four per treatment). Gravimetric soil moisture was measured weekly from three samples per quadrant. Measurements were taken at 5–15 cm depth to ensure sampling at the rooting depth.

### SUBALPINE TRANSPLANT

A second experiment was simultaneously implemented to test for differences between typical alpine tundra populations and those growing near the species' lower range limit. In this "subalpine transplant" experiment, an additional 648 adult *P. diversifolia* plants were collected from three populations in the subalpine zone (approximately 3000 m elevation) in the same manner and time frame as described above. This lower altitude site consisted of a moist late-melting meadow within a matrix of early- and late-melting sites dominated by a patchwork of alpine-tundra and subalpine vegetation. Plants originating in the subalpine populations were evenly divided among randomly assigned positions in the same below-range gardens described above, and three additional gardens within the native, subalpine range. At each location, subalpine populations received the same snowmelt and neighbor removal treatments as the alpine populations. Comparisons of plant performance were made between the alpine and subalpine populations in 1997.

## Statistical Analyses

Seasonal averages for leaf area and growth interval were compared using analysis of variance (JMP Software Version 4, SAS Institute, Inc., Cary, NC). The model included the fixed main effects: year, transplant location (native-range vs. below-range), treatment (unmanipulated, delayed snowmelt, and neighbor removal), and all interaction terms. The crossed effect of year × location × treatment was used as the denominator mean square in the *F* test for effects of treatment, year, and year × treatment. A repeated measures model was not used in this study because responses of individual plants were not assumed to be parallel from year to year (Sokal and Rohlf, 1995,

TABLE 1

1996 and 1997 mean snowmelt dates for the alpine transplant experiment. Average dates of snow disappearance at 12 replicate points within each treatment: unmanipulated, experimentally delayed snowmelt, and neighbor removal. Location names are: Native Range—transplant gardens within the species' native range (alpine); and Below Range—transplant gardens below the native range. See text for snowmelt dates in native subalpine plots.

	1996	1997
Native Range		
Unmanipulated	4 July	7 July
Neighbor removal	5 July	6 July
Delayed snowmelt	15 July	14 July
Below Range		
Unmanipulated	28 May	9 June
Neighbor removal	30 May	10 June
Delayed snowmelt	26 June	30 June

pp. 345–346). Tukey's HSD post-hoc analyses were applied to significant effects when comparisons among treatments were necessary. Weekly environmental data were plotted against date. Seasonal averages for temperature and soil moisture were compared each year with a two-way analysis of variance model for the fixed effects of transplant location, treatment, and location × treatment. Percentage survival and reproduction were graphically compared among groups, and numbers of surviving and reproducing individuals were compared using Fisher's exact test (Sokal and Rohlf, 1995, pp. 734–736).

In a separate set of analyses, leaf area and growth intervals of plants from the alpine transplant and subalpine transplant populations were compared. The ANOVA model included the fixed main effects: transplant location (native-range vs. below-range), source population (alpine vs. subalpine), treatment (unmanipulated, delayed snowmelt, and neighbor removal), and all interaction terms. Following classical common garden transplant designs (Turesson, 1922; Clausen et al., 1948), populations were tested for ecotypic variation by comparing the phenotypic expression of individuals from distinct habitats grown together in a common environment. With this approach, differential performance of populations in the transplant gardens would signify genetically based differences among plants from contrasting habitats. Differences within and among populations, treatments, and transplant locations were compared with Tukey's HSD post-hoc analyses.

## Results

### ENVIRONMENTAL EFFECTS OF LOCATION AND TREATMENTS

Table 1 summarizes the annual mean snowmelt dates for each treatment in the alpine transplant experiment. In both years of the study, the delayed snowmelt treatment postponed snowmelt by 21–28 days in the below-range gardens but only by about 7–11 days in the native-range gardens due to difficulties securing the reflective tarps at the tundra sites. Figure 1 shows detailed soil moisture and temperature in the alpine transplant experiment in 1997. Mean soil moisture was 15%–30% higher in the native-range than below-range. Soil moisture was similar across treatments except for initially higher soil moisture in the delayed treatments in the native-range immediately following snowmelt (ANOVA,  $F_{loc} = 48.91$ ,  $P < 0.001$ ;  $F_{trt} = 12.13$ ,  $P = 0.001$ ;  $F_{loc \times trt} = 5.82$ ,  $P < 0.001$ ). Post-hoc analyses revealed that the effects of treatment and location × treatment on soil moisture were due entirely to the first three weeks of measurement. Mean temperatures ranged from 4–15°C lower in the native-range than below-range, but

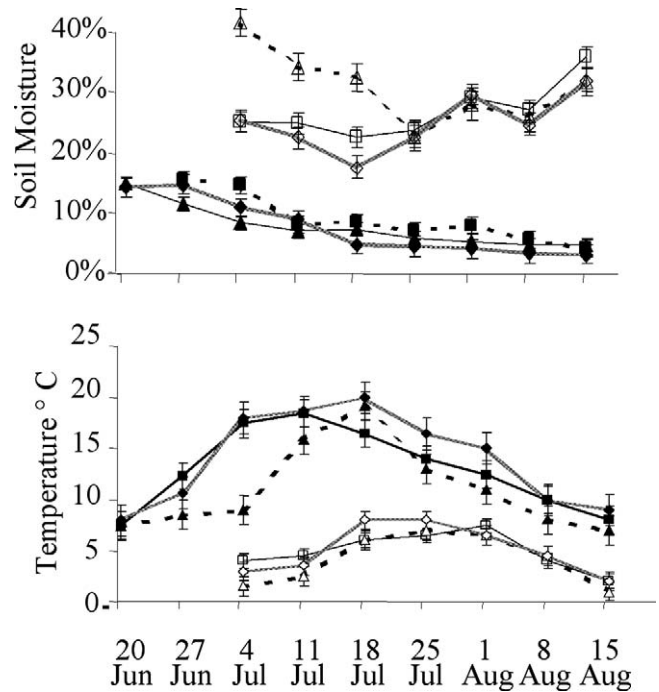


FIGURE 1. Weekly means and standard errors for soil temperature (°C) and gravimetric soil moisture taken from weekly averages at 12 points in each garden in 1997. N = 36. Open and closed symbols indicate native-range and below-range plots, respectively. Symbol legend: square symbol = unmanipulated treatment; triangle = delayed snowmelt; diamond = neighbor removal.

were similar among treatments in each location (ANOVA,  $F_{loc} = 86.21$ ,  $P < 0.001$ ;  $F_{trt} = 2.97$ ,  $P = 0.06$ ;  $F_{loc \times trt} = 0.45$ ,  $P = 0.77$ ). Post-hoc analyses indicated initially lower temperatures in the delayed treatments below the native-range. In the native subalpine gardens, mean snowmelt dates were ~9–10 days earlier than the alpine native gardens in each treatment (two-year averages—unmanipulated, June 28; neighbor removal, June 28; delayed snowmelt, July 5). Temperature and soil moisture patterns did not differ in the native alpine and native subalpine gardens in either year.

### ALPINE PLANT PERFORMANCE WITHIN AND BELOW THE NATIVE-RANGE

In the alpine transplant experiment, *P. diversifolia* had less than 15% survival in the below-range gardens compared to 70–80% survival in the native-range regardless of treatment (Fig. 2a). Reproduction was between 0% and 10% below-range and 10–15% in native-range (Fig. 2b). The neighbor removal treatment had a modestly positive influence on survival (Fisher's exact test,  $p < 0.05$ ) and reproduction ( $p < 0.05$ ) for the surviving plants in the below-range gardens. Fisher's exact tests demonstrated that the 1996 to 1997 decline in survival in the below-range gardens was not significant. Within the native-range gardens, survival and reproduction were similar in 1996 and 1997, and 10–20% of the surviving plants reproduced in all treatments. Survival in the native-range was reduced by 20–30% in the delayed snowmelt treatment compared to the other two treatments (Fisher's exact test,  $p < 0.05$ ). Thus, delayed snowmelt decreased performance within the native-range but did not affect survival or reproduction below the species range. High mortality below the species range far outweighed marginal responses to the neighbor removal treatment.



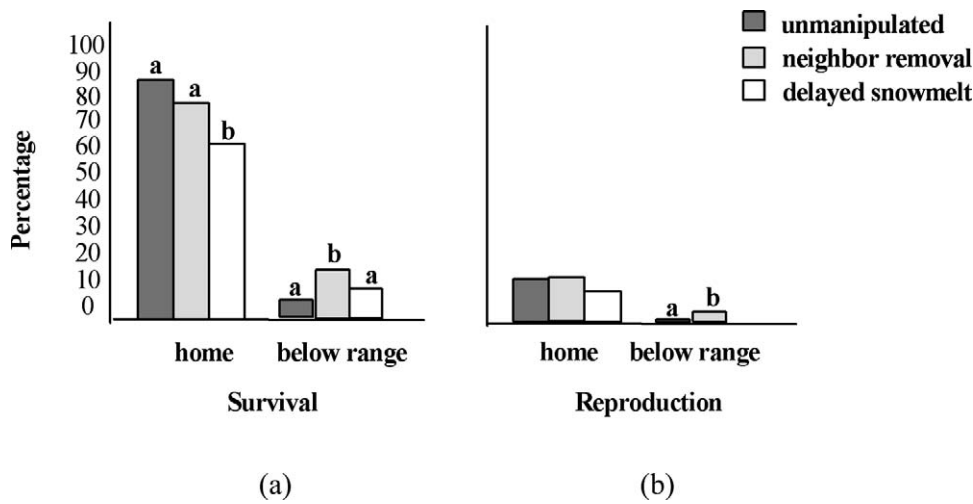


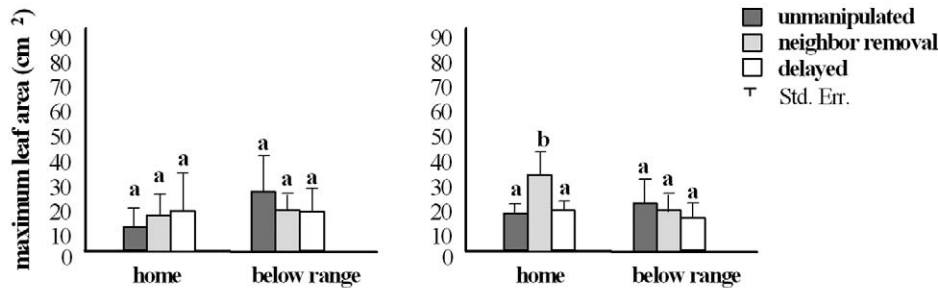
FIGURE 2. Percentage survival and reproduction of experimental plants within and below the native-range. Percent survival equals the number of individuals alive/total number transplanted; percent reproduction equals the number of individuals producing buds, flowers, or fruits/total number alive at the conclusion of the experiments in 1997. Different lowercase characters indicate significant Fisher's post-hoc tests at  $p < 0.05$  level. Initial N = 108 individuals per treatment.

Leaf area did not differ in the alpine transplant experiment between transplant locations or between years, but there was a treatment effect and a 3-way interaction effect among location, treatment, and year on leaf area (Fig. 3a, Table 2a). Post-hoc analyses showed that this variation was due to a 15–25 cm<sup>2</sup> increase in leaf area in the neighbor removal treatments within the alpine native-range gardens in 1997 (Tukey's post-hoc tests for neighbor removal versus delayed treatment,  $p = 0.03$ ; neighbor removal versus unmanipulated treatment,  $p < 0.01$ ), but not below the species range. Leaf area was similar between years for all other treatments.

Alpine populations increased the growth interval by approximately 10–15 days when transplanted below-range compared to the native-range in both years, but this response varied somewhat among

treatments and years (Fig. 3b, Table 2b). The delayed snowmelt treatments reduced the growth interval by 10–20 days in both locations and years compared to the unmanipulated treatments (Tukey's post-hoc tests,  $p < 0.05$ ), indicating that later snowmelt curtails the time available for active growth both within and below the species' range. The neighbor removal treatments reduced the growth interval by about 10 days compared to the unmanipulated treatment (Tukey's post-hoc tests,  $p < 0.05$ ) within the native-range, but did not alter the growth interval in the below-range gardens. The resulting treatment  $\times$  location interaction term therefore indicated significant effects of neighbor removal only within the native-range. Growth intervals were similar between years except in the unmanipulated treatment, in which growth intervals were longer in the earlier snowmelt year, 1997 ( $p < 0.01$ ).

### (a) Plant size



### (b) Growth interval

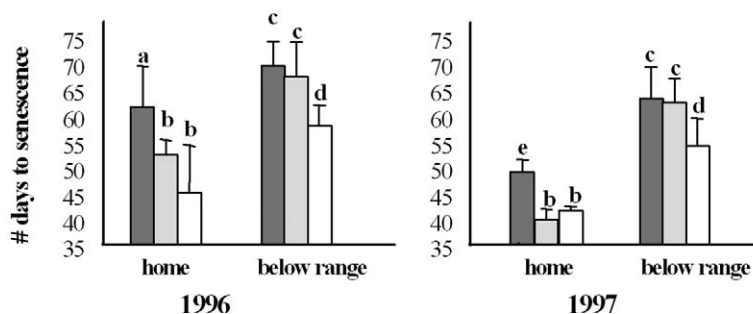


FIGURE 3. Means and standard errors for: (a) maximum leaf area (cm<sup>2</sup>) and (b) growth interval (number of days from emergence to senescence) in *P. diversifolia*. Different lowercase characters represent significant differences as follows: Tukey's post-hoc  $p$ -values for comparisons among the three treatments; Tukey's post-hoc  $p$ -values from 3-way ANOVA (Table 2) for comparisons between years.

The subalpine and alpine populations demonstrated differential performance within their native-ranges, but similar performance below the species' natural range (Fig. 4, Table 3). Populations from the subalpine zone had ~40 cm<sup>2</sup> greater leaf area and ~10 days longer growth intervals than alpine tundra plants in the native, unmanipulated treatments, indicating that these lower altitude sites are favorable for growth in this species. Subalpine populations also had ~25–30 cm<sup>2</sup> greater leaf area and ~3–6 days longer growth intervals in the other two treatments within the native-range but did not differ in size from alpine populations below the species' range. Alpine populations demonstrated a somewhat greater increase in growth intervals below the species' range limit than subalpine populations in most of the treatments. A significant location × population effect in the analysis of variance was attributable to greater leaf area and longer growth intervals in subalpine vs. alpine populations. However, leaf area was reduced and the growth interval was generally longer for both populations below the species' range than within the native-range, regardless of the source habitat. Thus, subalpine populations grew larger and for a longer period of time than alpine populations within their native sites, but both populations demonstrated plastic responses to the immediate environment and there was no evidence that lower-altitude populations were better adapted to below-range conditions than the alpine populations.

### Discussion

Based on theoretical expectations that biotic factors control the lower altitudinal limits of alpine plants (Dahl, 1951; Daubenmire, 1954; Billings and Bliss, 1959; Tranquillini, 1964; Hoffman and Blows, 1994), I predicted that neighbor removal rather than delayed snowmelt timing would enhance the performance of the alpine/high subalpine plant, *P. diversifolia* when transplanted below its normal range. However, this species' low survival in all treatments within the below-range gardens suggests instead that factors other than snowmelt timing or neighbor density directly affect survival at lower altitudes. Since neither treatment consistently altered environmental conditions within the experimental gardens, it is likely that low soil moisture and higher temperatures differences were the critical factors contributing to mortality below the species' natural range. While modest effects of neighbor removal on survival and reproduction in the below-range gardens suggest that vegetation cover may interact with temperature and soil moisture within a given microsite, the results argue that abiotic factors are much better predictors of lower distribution limits in this species than biotic interactions with neighbors. Recent experimental studies report that competition at low elevations restricts higher altitude species from lower altitudes (Choler et al., 2001; Heegaard, 2002). However, similar work in a high-latitude system demonstrated that abiotic conditions rather than biotic interactions were most important for determining tussock tundra species distributions (Hobbie et al., 1999). This paper contrasts with earlier generalizations that biotic factors set lower range limits in high-altitude plants, and lends additional empirical evidence to the prediction that temperature is a primary factor controlling upper and lower altitudinal range limits (Dahl, 1951; Grabherr et al., 1994; Pauli et al., 1999).

As shown for a number of other alpine plants, *P. diversifolia*'s high mortality below the species' range is likely to reflect physiological constraints on growth in warmer, drier microsities (Osmond et al., 1987; Stenstrom et al., 1997; Arft et al., 1999; Galen and Stanton, 1999; Walker et al., 1999; Bruelheide and Lieberum, 2001; Weih and Karlsson, 2002). In addition, accelerated developmental and reproductive cycles in this species have been shown to be adaptive in

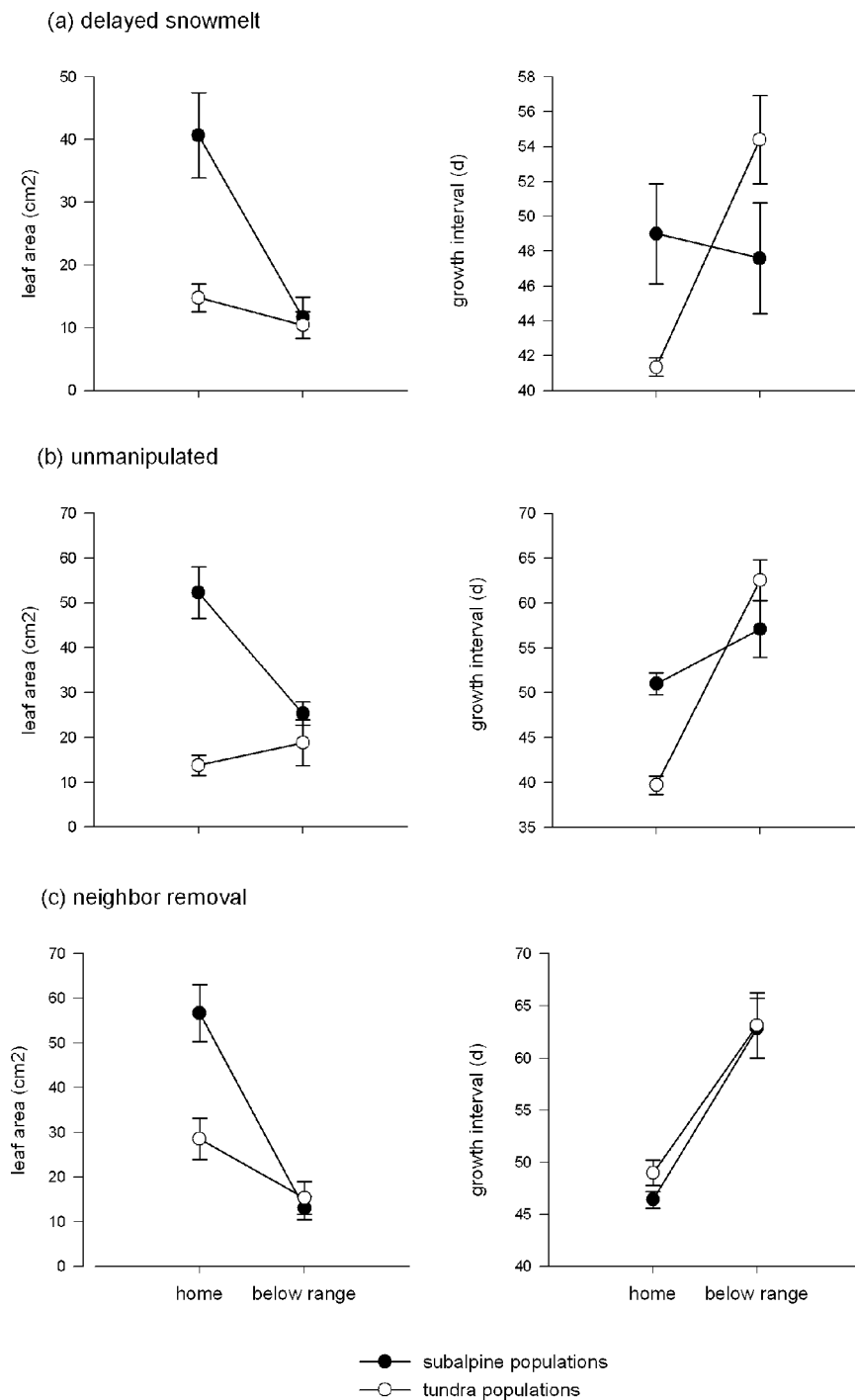
TABLE 2

ANOVA results for effects of transplant location, experimental treatment, and year on the size and growth interval of alpine populations of *P. diversifolia* transplanted within and below its range. Tukey's post-hocs for unequal N are noted in the text where appropriate. Initial N for each specie's and transplant location = 108 plants.

Effect	A. Leaf area (cm <sup>2</sup> )			B. Growth interval (# days)		
	MS Err	F	P	MS Err	F	P
Location	285.58	0.34	NS	57.86	197.78	≪0.01
Treatment	285.58	4.89	<0.01	57.86	32.82	≪0.01
Year	285.58	0.11	NS	57.86	46.27	≪0.01
Loc × Trt	285.58	0.40	0.01	57.86	7.28	<0.01
Loc × Yr	285.58	6.19	NS	57.86	9.20	NS
Trt × Yr	285.58	0.17	NS	57.86	1.47	NS
Loc × Trt × Yr	285.58	4.76	<0.01	57.86	0.85	NS

short growing seasons (Stinson, 1998), but may involve metabolic costs and water loss in warmer and drier conditions (Galen and Stanton, 1991). Indirect effects of other factors on growth and fecundity may also be important for the observed responses of *P. diversifolia* to experimental treatments. Although clipping vegetation probably reduced both root and shoot activity, the neighbor removal treatment may have had different and undetectable effects on below-ground interactions. Above-ground cover is notably lower in *P. diversifolia*'s alpine habitat than in the subalpine zone but it is possible that below-ground competition is important for both alpine and subalpine flora (Griggs, 1956; Theodose and Bowman, 1997). In addition, shading and/or sheltering effects of vegetation, and differences in community and soil albedo may have affected temperature as well as other, less obvious microclimatic variables not measured here (Bowman and Turner, 1993; Gottfried et al., 1998; Arft et al., 1999; Callaway et al., 2002).

Although abiotic factors are clearly important for this species, *P. diversifolia* did not demonstrate the commonly noted affinity of alpine species for late-melting sites per se (e.g., Scherff et al., 1994). Within the native-range, delayed snowmelt reduced survival and shortened *P. diversifolia*'s growth interval, suggesting instead that locally early-melting sites, when combined with sufficient soil moisture and cooler temperatures, are more favorable. Many other high-altitude species respond to longer growing seasons by extending the growth interval at earlier-melting portions of natural snowmelt gradients or in early snowmelt years, resulting in higher fecundity and/or survival in locally early-melting sites (see Körner, 1999). It is therefore not surprising that populations from lower altitudes demonstrated greater size and longer growth intervals than those from higher altitudes within the native-range. However, while ecotypic variation across altitudes is very well documented (Turesson, 1922; Clausen et al., 1948; Gurevitch, 1992; Stanton et al., 1997), there was no evidence that different factors control *P. diversifolia*'s distribution in different parts of its range. When transplanted below the native-range, the subalpine and alpine populations both expressed reduced leaf area despite an extended growth interval, irrespective of neighbor density or snowmelt treatments. Thus, both traits appear to be plastic in this species, exemplifying the ability to persist at smaller size on the alpine tundra and to elongate growing periods in earlier-melting sites. Such "tolerance plasticity" has been cited as a potential mechanism for broad distribution of other plants in suboptimal habitats (Jurjavec et al., 2002). Although elongation of the growth interval was not accompanied by increased size below the native-range, plasticity in this trait may be adaptive in locally earlier-melting sites within the native-range (Stinson, 2004).



**FIGURE 4.** Population-level mean values and standard errors for maximum leaf area and growth interval of alpine tundra and upper subalpine plants transplanted within and below the native-range. Native and below-range locations for each population are described in the text.

In conclusion, this study supports the general prediction that global changes in precipitation and temperature that affect snowmelt patterns will alter plant species' distributions at high elevations (Grabherr et al., 1994; Houghton et al., 1996; Körner, 1999; Walker et al., 1999), but does not support the hypothesis that interference with subalpine vegetation will restrict the alpine plant *P. diversifolia* from lower altitudes. Clearly, neighbor density and snowmelt timing were both less important for setting lower altitudinal limits than the direct effects of other subalpine microsite factors on survival. While experimental manipulations of snowmelt timing are not always realistic proxies for climate change in high-altitude regions (Galen and Stanton, 1993; Pauli et al., 1999; Price and Waser, 2000), the present study offers empirical evidence that abiotic factors currently restrict

*P. diversifolia* to cooler and wetter sites. Therefore, the predicted encroachment of the subalpine flora (Holten, 1993; Emmanuel et al., 1995) is less likely to displace this species than the overwhelmingly negative effects of abiotic controls on its distribution. *P. diversifolia*'s performance within its native habitat further supports the idea that changes in the snowmelt regime can result in transient positive responses, followed by reduced growth and species loss (Arft et al., 1999; Walker et al., 1999). Because this species currently performs better in the earlier-melting parts of its range, it may undergo initial, positive responses to earlier snowmelt prior to drought and/or temperature induced mortality. In addition, reduced precipitation is likely to mitigate the benefits of earlier snowmelt to high-altitude plants, thereby slowing the predicted up-slope migration of both

TABLE 3

**F ratios and model for effects of transplant location, population, and experimental treatments on size and growth interval of *P. diversifolia* transplanted from alpine tundra and upper subalpine zones. Tukey's post-hocs for unequal N are noted in the text where appropriate. Initial N for each species' and transplant location = 108 plants.**

Effect	A. Leaf area (cm <sup>2</sup> )			B. Growth interval (# days)		
	MS Err	F	P	MS Err	F	P
Location	227.78	46.78	<0.01	52.34	87.73	<0.01
Population	227.78	35.66	<0.01	52.34	0.25	0.62
Treatment	227.78	4.340	0.01	52.34	9.92	<0.01
Loc × Pop	227.78	28.15	<0.01	52.34	14.47	<0.01
Loc × Trt	227.78	3.84	0.02	52.34	5.26	<0.01
Trt × Pop	227.78	1.24	0.29	52.34	1.08	0.34
Loc × Pop × Trt	227.78	0.15	0.86	52.34	5.61	<0.01

subalpine and alpine species (Pauli et al., 1999; Price and Waser, 2000). Whether or not subalpine vegetation advances upslope, higher temperatures and/or droughts accompanying advanced snowmelt may lead to range retraction in *P. diversifolia* as suitable alpine habitat recedes.

### Acknowledgments

The author thanks D. A. Stratton and H. S. Horn for research guidance; E. Baumgartner, S. Borges, M. Lett, E. Mathai, and D. Wallace-Senf for invaluable field assistance; the members and staff of Rocky Mountain Biological Laboratory (RMBL) for logistical and research support; and T. Seidler, S. Catovsky, M. Lerdau, G. Motzkin, and two anonymous reviewers for comments on the manuscript. E. Sudderth and K. Wolfe-Bellin provided helpful editorial comments. Funding was provided to the author by NSF (DEB-9520859) and a RMBL Graduate Research Scholarship.

### References Cited

- Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jonsdottir, I. S., Laine, K., Levesque, E., Marion, G. M., Molau, U., Molgaard, P., Nordenhall, U., Raszhivin, V., Robinson, C. H., Starr, G., Stenstrom, A., Stenstrom, M., Totland, O., Turner, P. L., Walker, L. J., Webber, P. J., Welker, J. M., and Wooley, P. A., 1999: Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, 69: 491–511.
- Billings, W. D., and Bliss, L. C., 1959: An alpine snowbank environment and its effects on vegetation, plant development and productivity. *Ecology*, 40: 389–397.
- Bliss, L. C., 1962: Adaptations of arctic and alpine plants to environmental conditions. *Arctic*, 15: 117–144.
- Bliss, L. C., 1985: Alpine. In: Chabot, B. F., and Mooney, H. A. (eds.), *Physiological Ecology of North American Plant Communities*. New York: Chapman and Hall, 41–65.
- Bowman, W. D., and Turner, L., 1993: Photosynthetic sensitivity to temperature in populations of two C4 *Bouteloua* (Poaceae) species native to different altitudes. *American Journal of Botany*, 80: 369–374.
- Box, E. O., 1995: Factors determining distributions of tree species and plant functional types. *Vegetatio*, 121: 101–116.
- Bruehlheide, H., and Lieberum, K., 2001: Experimental tests for determining the causes of the altitudinal distribution of *Meum athamanticum* Jacq. in the Harz Mountains. *Flora*, 196: 227–241.
- Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. L., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., and Cook, B. J., 2002:

- Positive interactions among alpine plants increase with stress. *Nature*, 417: 844–848.
- Choler, P., Michalet, R., and Callaway, R. M., 2001: Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82: 3295–3308.
- Clausen, J., Keck, D., and Hiesey, W., 1948: *Experimental studies on the nature of species. III. Environmental responses of climatic races of Achillea*. Carnegie Institution of Washington Publication 581.
- Connell, J. H., 1961: The influence of intraspecific competition and other factors on the distribution of the barnacle *Cthamulus stellatus*. *Ecology*, 42: 710–723.
- Dahl, E., 1951: On the relation between summer temperature and the distribution of alpine vascular plants in the lowlands of Fennoscandia. *Oikos*, 3: 22–52.
- Daubenmire, R., 1954: Alpine timberlines in the Americas and their interpretation. *Butler University Botanical Study*, 11: 119–136.
- Emmanuel, W. R., Shugart, H. H., and Stevenson, M. P., 1995: Climatic change and the broadscale distribution of terrestrial ecosystem complexes. *Climatic Change*, 7: 29–43.
- Galen, C., 1990: Limits to the distributions of alpine tundra plants: herbivores and the alpine skypilot, *Polemonium viscosum*. *Oikos*, 59: 355–358.
- Galen, C., and Stanton, M. L., 1991: Looking before you leaf: divergence in allocation strategies within a population of the alpine buttercup, *Ranunculus adoneous*. *American Journal of Botany*, 78: 56.
- Galen, C., and Stanton, M. L., 1993: Short-term responses of alpine buttercups to experimental manipulations of growing season length. *Ecology*, 74: 1052–1058.
- Galen, C., and Stanton, M. L., 1999: Seedling establishment in alpine buttercups under experimental manipulations of growing-season length. *Ecology*, 80: 2033–2044.
- Gottfried, M., Pauli, H., and Grabherr, G., 1998: Prediction of vegetation patterns at the limits of plant life: A new view of the alpine-nival ecotone. *Arctic and Alpine Research*, 30: 207–221.
- Grabherr, G., Gottfried, M., and Pauli, H., 1994: Climate effects on mountain plants. *Nature*, 369: 448–448.
- Grace, J., 1987: Climatic tolerance and the distribution of plants. *New Phytologist*, 106: 113–130.
- Griggs, R. F., 1956: Competition and succession in a Rocky Mountain fellfield. *Ecology*, 37: 8–20.
- Grime, J., 1979: *Plant Strategies and Vegetation Processes*. London: John Wiley.
- Gurevitch, J., 1992: Differences in photosynthetic rate in populations of *Achillea lanulosa* from two altitudes. *Functional Ecology*, 6: 568–574.
- Heegaard, E., 2002: A model of alpine species distribution in relation to snowmelt time and altitude. *Journal of Vegetation Science*, 13: 493–504.
- Hobbie, S., Shevtsova, A., and Chapin, F., 1999: Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos*, 84: 417–434.
- Hoffman, A. A., and Blows, M., 1994: Species borders: ecological and evolutionary perspectives. *Trends in Ecology and Evolution*, 9: 223–226.
- Holderidge, L. R., 1967: *Life Zone Ecology*. San Jose, Costa Rica: Tropical Science Center.
- Holten, J. I., 1993: Potential effects of climatic change on distribution of plant species, with emphasis on Norway. In: Holten J. I. et al. (eds.), *Impacts of climatic change on natural ecosystems*. Trondheim, Norway: Norwegian Institute for Nature Research.
- Houghton, J. T., Meira Filho, L. G., Callander, B. A., Harris, N., Kattenberg, A., and Maskell, K., 1996: *Climate change 1995: the science of climate change*. Cambridge, UK: Cambridge University Press.
- Jurjavac, N. L., Harrison, S., and Wolf, A. T., 2002: Abiotic stress, competition, and the distribution of the native annual grass *Vulpia microstachys* in a mosaic environment. *Oecologia*, 130: 555–562.
- Körner, C., 1999: *Alpine Plant Life: functional plant ecology of high mountain ecosystems*. New York: Springer-Verlag.



- Kudo, G., and Ito, K., 1992: Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan. *Vegetatio*, 98: 165–174.
- MacArthur, R. H., 1972: *Geographical ecology: Patterns in the distribution of species*. New York: Harper and Row.
- Osmond, C. B., Austin, M. P., Berry, J. A., Billings, W. D., Boyer, J. S., Dacey, J. W. H., Nobel, P. S., Smith, S. D., and Winner, W. E., 1987: Stress physiology and the distribution of plants. *Bioscience*, 37: 38–48.
- Pauli, H., Gottfried, M., and Grabherr, G., 1999: Vascular plant distribution patterns at the low-temperature limits of plant life—the alpine-nival ecotone of Mount Schrankogel (Tyrol, Austria). *Phytocoenologia*, 29: 297–325.
- Price, M. V., and Waser, N. M., 2000: Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications*, 10: 811–823.
- Scherff, E. J., Galen, C., and Stanton, M. L., 1994: Seed dispersal, seedling survival and habitat affinity in a snowbed plant: limits to the distribution of the snow buttercup, *Ranunculus adoneous*.
- Sokal, R. R., and Rohlf, F. J., 1995: *Biometry*. Third Edition. New York: W. H. Freeman and Company.
- Stanton, M. L., Rejmanek, M., and Galen, C., 1994: Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, U.S.A. *Arctic and Alpine Research*, 26: 364–374.
- Stanton, M. L., Galen, C., and Shore, J., 1997: Population structure along a steep ecological gradient: consequences of flowering time and habitat variation in the snow buttercup, *Ranunculus adoneous*. *Evolution*, 51: 79–94.
- Stenstrom, M., Gugerli, F., and Henry, G. H. R., 1997: Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. *Global Change Biology*, 3: 44–54.
- Stinson, K. A., 1998: Effects of snow-melt timing on three high altitude *Potentilla* species: growth, reproduction, and distribution. Ph.D. Thesis, Princeton University, Princeton, New Jersey, 170 pp.
- Stinson, K. A., 2004: Natural selection favors rapid reproductive phenology in *Potentilla pulcherrima* (Rosaceae) at opposite ends of a subalpine snowmelt gradient. *American Journal of Botany*, 91: 531–539.
- Theodose, T. A., and Bowman, W. D., 1997: The influence of interspecific competition on the distribution of an alpine graminoid: evidence for the importance of plant competition in an extreme environment. *Oikos*, 79: 101–114.
- Tranquillini, W., 1964: Physiology of plants at high altitudes. *Annual Review of Plant Physiology*, 15: 345–362.
- Turesson, G., 1922: The genotypical response of the plant species to the habitat. *Hereditas*, 3: 147–236.
- Walker, D. A., Halfpenny, J. C., Walker, M. D., and Wessman, C. A., 1993: Long term studies of snow-vegetation interactions. *Bioscience*, 43: 287–301.
- Walker, M. D., Walker, D. A., Welker, J. M., Arft, A. M., Bardsley, T., Brooks, P. D., Fahnestock, J. T., Jones, M. H., Losleben, M., Parsons, A. N., Seastedt, T. R., and Turner, P. L., 1999: Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes*, 13: 2315–2330.
- Weber, W., and Wittmann, R., 1996: *Colorado Flora: Western Slope*. Revised Edition. Niwot, CO, U.S.A.: University Press of Colorado.
- Weih, M., and Karlsson, P. S., 2002: Low winter soil temperature affects summertime nutrient uptake capacity and growth rate of mountain birch seedlings in the subarctic, Swedish lapland. *Arctic Antarctic, and Alpine Research*, 34: 434–439.
- Woodward, F. I., and Williams, B. G., 1987: Climate and plant distribution at global and local scales. *Vegetatio*, 69: 189–197.

Revised ms submitted September 2004