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Nurse Effects of Alpine Willows (*Salix*) Enhance Over-winter Survival at the Upper Range Limit of Fireweed, *Chamerion angustifolium*

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Abstract

Shrubs may act as nurse plants by facilitating the establishment and/or survival of under-story herbaceous plants under stressful conditions. Such interactions may promote the movement of montane species into alpine plant communities. We studied potential nurse effects of alpine willow shrubs (*Salix* spp.) on fireweed (*Chamerion angustifolium*) at three life history stages: seed, established seedling, and adult. Mechanisms for nurse effects were assessed at each stage by placing transplants into modified microsites containing shade and wind protection, as well as into unmanipulated microsites in open meadow and willow under-story habitats. Seedling establishment occurred only under the willow canopy and even there was extremely rare. Willows and experimental microcosms that simultaneously increased shade and reduced wind velocity strongly promoted over-winter survival of established seedlings and adults. All adult transplants surviving over the winter persisted over the subsequent growing season. For seedling transplants, extremely high mortality in exposed plots over the winter limited our power to experimentally detect nurse effects during the next growing season. Results suggest that by promoting persistent snow cover over the winter, willows enhance survival of fireweed at its upper range limit, potentially favoring its spread into alpine habitats.

Introduction

As plants coexist in close proximity, neighbors alter the availability of limiting resources including water, light, and nutrients. Competition has historically been the main focus of studies on plant-plant interactions (Gleason, 1926; Grace and Tilman, 1990); however, a growing body of literature supports the importance of facilitation, especially in habitats characterized by intense environmental stress (Connell and Slatyer, 1977; Callaway, 1995; Bertness and Callaway, 1994; Levine, 2001; Miriti et. al., 2001). Nurse effects, in which a plant provides neighbors with shelter from abiotic stress, are an important subset of facilitative relationships. Nurse plants can promote growth, establishment, and survival of recipient plants by increasing relative humidity, buffering temperature extremes, shielding shoot tissue from intense irradiation and strong winds, and reducing herbivore attack (Callaway, 1995; Brooker and Callaghan, 1998; Stachowicz, 2001).

Because facilitator species may expand the ecological niche of beneficiary plant species, nurse effects can bring about the establishment of new species and in so doing promote community succession and biological invasion (Connell and Slatyer, 1977; Maron and Conners, 1996; Richardson et al., 2000; Bruno et al., 2003; Lenz and Facelli, 2003; Cavieres et al., 2005a). Potential outbreaks of non-native species with weedy characteristics, as well as aggressive native species from adjacent habitats, are of concern because of their potential to disrupt ecological communities (Williamson, 1996). With global climate change, cold refugia for true alpine organisms are warming and, consequently, alpine species may be displaced as dominant or invasive species move up from lower elevations (Theurillat and Guisan, 2001; Korner, 2003; Krajick, 2003).

For plant species to cross the ecotone between subalpine and alpine habitats, individuals must have mechanisms to establish and persist in an environment where harsh conditions year-round limit growth and survival. In the winter months, strong winds, low ambient temperatures, and extreme temperature fluctuations lead to desiccation and disturbance from frost heave. In the summer, intense irradiation, nutrient and moisture limitation, and short growing seasons constrain growth (Bliss, 1956; Billings and Mooney, 1968; Ehleringer and Miller, 1975; Enquist and Ebersole, 1994; Körner, 2003).

Given the adversity of alpine habitats, facilitation may represent a key process in determining species distributions, community composition, and rate of species turnover due to immigration from lower elevations (Nunez et al., 1999; Cavieres et al., 2002, 2005a, 2000b; Arroyo et al., 2003). At high elevations, facilitative relationships between native alpine plant species have been revealed by mapping species distributions (e.g., Kleier and Lambrinos, 2005) and by conducting neighbor removal and transplant experiments (Choler et al., 2001; Totland and Esaete, 2002; Callaway et al., 2002; Castro et al., 2004). Here we test for nurse effects of alpine willows (*Salix*, Salicaceae) at the upper range limit of the predominantly subalpine species *Chamerion angustifolium* L. (Onagraceae, fireweed). Experiments were designed to (1) test for facilitation during seed, seedling, and adult life stages, and (2) identify the mechanism(s) and seasonal timing of nurse effects.

STUDY SYSTEM

Willows (*Salix*) are a prominent component of alpine vegetation in Europe and North America, modifying snowmelt patterns, exposure, and soil chemistry in krummholz habitats (Holtmeier and Broll, 1992; Jumpponen et al., 1998). Jonasson (1992) observed decreased projected plant area (PPA) in the

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understory species *Vaccinium myrtillus* after removal of *Salix* or *Betula* canopy species, consistent with facilitative effects in the Arctic. Similarly, in Norway, Totland and Esaete (2002) found decreased biomass of 15 herbaceous understory species after *Salix* canopy removal. In our study area on Pennsylvania Mountain in the central Rocky Mountains (Park County, Colorado, U.S.A.; 39°15′N, 106°06′W), the krummholz is made up of two willow species, S*alix glauca* L. and *S. brachycarpa* Nutt, and their hybrids. Shrubs are deciduous and erect, growing to 0.5–1.5 m in height and diameter.

Chamerion angustifolium L., fireweed, is a circumboreally distributed herbaceous perennial with a predominantly subalpine distribution in the central Rocky Mountains. Fireweed occasionally extends up into the willow under-story and open meadows of the alpine krummholz. Because of its weedy characteristics and proximity to the alpine, fireweed is a species of concern. In the past half century, *C. angustifolium* has extended its altitudinal range into new alpine habitats in the Rocky Mountains (Galen, personal observation) and Scandinavian Alps (Lagerstrom, 2003). Plants of *C. angustifolium* reproduce sexually and vegetatively by rhizomatous growth. Shoot buds formed on the rhizomes in the fall initiate growth after snowmelt in the early summer (Myerscough, 1980). Mature plants produce racemes of pink-purple flowers that are typically animal-pollinated but capable of self pollination. A single large ramet may produce hundreds of seed capsules that each contain up to 500 seeds, giving rise to as many as 80,000 seeds in one year (Myerscough, 1980). Seeds of *C. angustifolium* are small, wind-dispersed, and lack dormancy (Myerscough, 1980; Granstrom, 1982). Solbreck and Andersson (1987) found that a large proportion of fireweed seeds (20–50%) are carried 100 m or more above the ground. When coupled with an average fall time of 0.065–0.069 m s^{-1} in still air, seeds are capable of attaining dispersal distances of hundreds of kilometers. If established *C. angustifolium* seedlings do not experience sufficient growth to form an underground shoot bud before winter, they must persist through the winter with leaf tissue exposed above ground. Under all conditions, fireweed undergoes vigorous mortality at the seedling stage (Myerscough, 1980; Wood and Morris, 1990; Stocklin, 1992). Consequently, recruitment in *C. angustifolium* is likely to be limited by safe sites rather than seed number or dispersal.

Materials and Methods

STUDY SITE

Experiments were performed in the krummholz (upper tree-limit) zone between 3560–3600 m elevation on Pennsylvania Mountain. In this area, willows are distributed as isolated individuals and in clumps within grassy alpine meadows. Fireweed occurs naturally but sparsely within the willow canopy and nearby open meadow vegetation. The study was conducted from May 2003 to June 2005.

NURSE EFFECTS DURING SEEDLING ESTABLISHMENT

In August 2003, seeds of *C. angustifolium* were haphazardly collected from five or more plants in each of two alpine populations (39°15′N, 106°06′W, and 39°15′N, 106°08′W) on Pennsylvania Mountain and one nearby montane population (39°12′N, 106°02′W) within 10 km of the study site. Seed comb was removed from the seeds by gentle mechanical agitation. Seeds from the three source populations were combined in bulk. In early September, batches of 40 seeds were taken from the bulk mixture and assigned at random among one hundred 0.15 m × 0.2 m seed grids in a 50 m × 60 m study area on Pennsylvania Mountain. Twenty seed grids were placed in random locations under the willow canopy and the other eighty were placed at random in open meadow vegetation (within 1–10 m of a willow). Grids were constructed of plastic, and each contained 140 walled but open-bottomed, square cells of 2.25 cm^2 area. Vegetation in destination microsites was left intact except where disturbance was necessary to ensure that the 40 cells at the center of each grid lay flat on the ground. The 40 seeds in each batch were placed individually in these central cells. A subsample of seeds was retained and germinated in the greenhouse at the University of Missouri–Columbia to verify viability.

In May 2004, before the onset of seed germination, grids in meadow vegetation ($n = 80$) were assigned evenly among four treatments in a randomized design: shade, wind block, shade plus wind block, and control (no manipulation). Black shade cloth (Easy Gardner, Inc., Waco, Texas; Heavy Black—75% shade) was suspended 0.3 m above the ground on four wire poles and draped over a platform (0.3 m × 0.4 m) made of hardware cloth. The shade treatment closely approximated the average leaf area index (LAI) beneath the willow canopy (LAI ≈ 1.8; LI-COR 2000 LAI meter, LI-COR, Inc., Lincoln, Nebraska). Wind blocks were created by attaching pieces of Double Polished Super Clear Vinyl (Nordic Shield Plastic Corp., Oxford, Massachusetts; 8990 Heavy; 0.3 m ht × 0.8–1 m length) to three wooden stakes. Stakes and plastic formed a "V" facing west to provide maximum shielding from the dominant winds. Grids were censused twice weekly through 26 August and weekly through 11 September 2004 for germination and survival. Cells containing seedlings were marked with plastic toothpicks. If the species identity of a seedling was uncertain, it was photographed, tracked until large enough for verification, and compared with other known fireweed seedlings. The number of seedlings emerging per grid and surviving through 11 September 2004 was recorded for each plot. Entry of naturally occurring seeds from the seed bank or during dispersal was not prevented. Instead, seed germination was monitored in cells to which no seeds were added as a check for background recruitment. At completion of the experiment, the top layer of soil from all seed grids was collected, transported to the greenhouse, potted, and watered to test for a residual seed bank.

NURSE EFFECTS ON ESTABLISHED SEEDLING AND ADULT SURVIVAL

In May–June 2003, fireweed seeds collected haphazardly in the populations described above as well as one additional montane population (39°21′N, 106°04′W) were germinated in the greenhouse, and the seedlings were grown until all produced true leaves. Because of low germination, additional seedlings with cotyledons or first true leaves were collected in the field from the same localities in June 2003. All seedlings were transplanted into a mixture of Pro-mix soil-less growth medium (Premier Horticulture Ltd., Quakertown, Pennsylvania) and sand (3:1 w:w) and grown until each had at least two true leaves. These and all other transplants (see below) were maintained for three weeks in a sheltered location adjacent to the study site to harden off before transplanting. Seedlings in this experiment are designated as "established" because each had true leaves before transplanting. Field and greenhouse-germinated seedlings were observed for differential mortality for two weeks after transplanting, but did not differ in average survival (paired t-test: $t = 0.51$, $p = 0.64$). Consequently, the two groups were merged for all analyses. A

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second set of established seedling transplants was conducted in 2004, using seeds from greenhouse grown plants. Parental plants were grown from seed collected on Pennsylvania Mountain in 2002 and were randomly mated in the winter, 2004. Seedling cultivation in 2004 followed methods described above.

Adult transplants in 2003 were grown from field-collected rhizomes. Rhizomes were taken from the two fireweed populations on Pennsylvania Mountain: (populations 1 and 2) and from three nearby montane populations (3: 39°12′N, 106°02′W; 4: 39°10′N, 106°03′W; and 5: 39°05′N, 105°24′W). After excavation, rhizomes were cut into 4-cm lengths, rooted with Rootone® Rooting Hormone (GardenTech, Inc., Lexington, Kentucky), and potted in a mixture of Pro-mix and sand.

Established seedlings (in both years) and rhizomes (2003) were randomly and evenly divided among five treatment groups (shade, wind block, shade plus wind block, control, and willow) and planted in 11 plots per treatment on Pennsylvania Mountain. Plots were located within the same 50 m × 60 m study area described above, within 0.5–5 m of seed germination grids. The shade cloth platforms (0.3 m × 0.4 m) were constructed of black shade cloth (Hummerts International, Inc., Earth City, Missouri; 70% neutral shade: LAI = 1.8) doubled over hardware cloth, which was elevated approximately 0.4 m above the ground on four wire poles. Wind blocks were constructed and oriented as described above.

In mid-July 2003 and 2004, seedlings were transplanted into separate holes, 5 cm deep × 1.2 cm in diameter. In so far as possible without damage, potting mix was removed from seedling roots before transplanting. In each experimental plot, the six seedlings representing each annual cohort were placed in holes separated by approximately 10 cm from one another and 15 cm from seedlings of the other annual cohort. On 14 July 2003, two shoots grown from rhizomes of unique source populations were transplanted into the same plots, separated by 15 cm from one another and 20 cm from seedlings. Transplants were covered with plastic sunhats for one week and watered daily for the first three days and every other day for the next four days. Established seedlings and adults that died within a week after transplanting were replaced with plants from the same source populations. It was not clear how to partition mortality that occurred during the first growing season between transplant effects and treatment effects. We took a conservative view and attributed mortality during this period to transplant shock. Accordingly, individuals dying during the first growing season were removed from the analysis. Survival of 2003 seedling and adult transplants was monitored over the winter (11 August 2003 to 3 July 2004) and over the following summer (to 11 September 2004). Survival of 2004 seedling transplants was monitored only over the winter (11 September 2004 to 24 June 2005). Wind block and shade structures were left in place through the entire experiment.

ENVIRONMENTAL CONDITIONS IN PLOTS CONTAINING ESTABLISHED SEEDLING AND ADULT TRANSPLANTS

To assess abiotic environmental conditions within treatments, soil moisture, light intensity, wind speed, and maximum temperature were measured in all plots containing seedling and adult transplants. On 13 July 2003, after three days without rain, soil cores (9 cm ht × 1.2 cm diam) were collected from transplant plots and stored in sealed plastic (Zip-lock) bags. Within 4 hours of collection, the soil samples were weighed, dried at 104°C for 24 hours, and weighed again. The soil bulk density was measured for each sample [(weight of the dry soil)/(volume of soil core) in g cm^{-3}], and relative water content (RWC) was calculated volumetrically as:

$$\frac{vol.water}{vol.soil} = \frac{wt.water}{wt.drysoil} \times \frac{bulkdensitysoil}{bulkdensitywater} \text{ (Gardener, 1965). (1)}$$

From 25 July to 8 August 2003, we measured photosynthetically active radiation (PAR), wind speed, and temperature in one randomly selected plot per treatment daily. The plots were randomly sampled without replacement on each day such that measurements were collected in all experimental plots over the entire two-week period. PAR was monitored five to seven times daily using Li-Cor (LI-190SB) quantum sensors attached to a CR-10 data logger (Campbell Instruments Inc.).

Wind speed was measured three times daily (9:00–10:30, 12:00–13:00, and 15:00–17:00 h) with a Turbometer (Davis Instruments, Hayward, California). The instrument was positioned vertically at ground level and oriented due west for 1 min. Maximum wind speed per sampling interval was averaged daily to estimate mean maximum wind speed for each plot. Air temperature was measured with HOBO data loggers (Onset Computer Corp., Bourne, Massachusetts) at 4-min or shorter intervals. Data loggers were placed under inverted Styrofoam cups with holes cut in the sides to permit air circulation and provide protection from direct sun. When possible, temperature samples were supplemented by placing data loggers in three additional plots (one per treatment, eight total per day). Deviation from the average daily maximum temperature was calculated for each plot. Rainfall was measured volumetrically on three days of heavy rain in the summer of 2004 by placing an 8 cm ht × 1 cm diam tube in the center of each plot.

STATISTICAL ANALYSIS

Nurse Effects during Seedling Establishment

Because of low and sporadic germination, data were not normally distributed, so we used separate Kruskal-Wallis nonparametric one-way ANOVAs to compare germination rate and the proportion of germinating seedlings which survived until the end of the 2004 growing season among treatments. For this and all other statistical analyses, the Statistical Analysis System (SAS) Version 6 software was used (SAS, Proc NPAR1WAY; SAS Institute, Inc., 2001).

Nurse Effects on Established Seedling and Adult Survival

Survival rates per plot were not normally distributed. Accordingly, for each annual cohort, we used separate Wilcoxon signed-rank tests to compare over-winter survival under the willow canopy to that in each of the other treatments. So few seedling transplants survived over the winter in several treatments that statistical analysis of survival trends over the subsequent growing season was not possible (see Results, Fig. 3). Variation among treatments and source populations in over-winter survival of adult plants was tested for significance using categorical analysis of variance (SAS, Proc CATMOD). All plants which survived over the winter also survived through the 2004 growing season, so statistical analysis of survival over the summer was deemed redundant. Zero values were coded with 0.01 to allow for maximum likelihood estimation of Chi-square statistics (SAS, 1989). The initial model tested effects of source population, treatment, and the source by treatment interaction on adult over-

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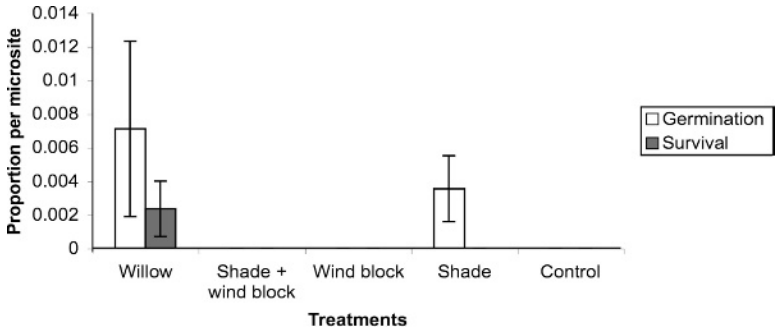


FIGURE 1. Rates of seed germination and seedling establishment for *Chamerion angustifolium* in different experimental treatments. Bars show treatment means, and error bars indicate standard errors.

winter survival. Because the source by treatment interaction was not significant ($P > 0.99$), it was removed from the final analysis.

Environmental Conditions in Experimental Plots

In the established plots containing seedling and adult transplants, variation in average wind speed, deviation from daily maximum temperature, PAR, volumetric soil moisture, and rainfall was analyzed by principal components analysis (PCA) (SAS, Proc FACTOR, Varimax rotation). Due to the absence of maximum temperature and rainfall measurements for a few plots, 46 of 55 observations were included in the analysis. Missing values were evenly distributed across treatments. Three principal components (factors) with eigenvalues > 1.0 were retained for comparison among treatments. Analysis of variance followed by planned contrasts was used to test for treatment effects on each factor (SAS, proc GLM) and to compare factor means in willow plots to those in open control and experimentally manipulated plots. Factor 2 data were non-normal. Non-parametric analyses (Wilcoxon tests) produced similar results as ANOVA, thus parametric statistics are reported for all three factors.

Results

NURSE EFFECTS DURING SEEDLING ESTABLISHMENT

Germination of seeds planted in September 2003 was extremely low. Of 4000 total seeds planted, only 11 seedlings emerged the following summer (0.275%). Two seedlings emerged within shade plots and 9 others under the willow canopy (Fig. 1). Greenhouse germination rates (34%) indicated moderate seed viability. No *C. angustifolium* seeds germinated in the greenhouse from grid soil samples collected after the experiment. Perhaps because germination was extremely rare in all treatments, the Kruskal-Wallis test for treatment effects on germination was non-significant ($p = 0.103$). Similarly, variation in survival of seedlings to establishment among treatments was non-significant (Wilcoxon, $p = 0.1066$). The few ($n = 4$) seedlings surviving until 11 September 2004 were all underneath willows.

NURSE EFFECTS ON ESTABLISHED SEEDLING AND ADULT SURVIVAL

Over-winter survival of 2003 seedling transplants was greatest in plots underneath willows and in plots characterized by shade plus wind block (Fig. 2A); in shade, open control and wind block treatments survival rates were significantly lower than under willows ($z > 2.0746$, $P < 0.038$ for all). However, survival under the shade plus wind block treatment was similar to that in the willow canopy ($z = 0.3916$, $P = 0.6953$). Over-winter survival of seedling transplants in 2004 showed similar trends. Survival rates under the willow canopy and in the shade plus wind block treatment were high and similar ($z = -0.6297$, $P = 0.5289$; Fig. 2B). Significantly lower over-winter survival occurred in the open and with wind block alone ($z > 2.251$, $P < 0.024$). Survival under the willow canopy also tended to be higher than survival in the shade though the difference was marginally significant ($z = 1.87$, $P = 0.0609$; Fig. 2B). Seedlings planted in 2003 that survived through the winter had high survival rates over the 2004 growing season in all treatments (Fig. 3).

The probability of adult survival varied significantly among treatments (Categorical ANOVA: $\chi^2_{df=4} = 10.88$, $P = 0.028$) and marginally with source population ($\chi^2_{df=4} = 8.62$, $P = 0.0712$). Transplants in the willow canopy had the highest survival (83%) followed by those protected by both shade and wind block (55%). Transplants in the open had the lowest over-winter survival rate (27%; Fig. 4). Planned contrasts for differences in adult survival between treatments showed that the probability of survival was significantly greater in the willow canopy than in open plots ($P = 0.0024$), plots characterized by shade ($P = 0.0054$), or plots equipped with wind blocks only ($P = 0.0284$). Survival was also higher in the willow canopy than in plots protected by both shade and wind block, but the planned contrast for this effect was only marginally significant ($P = 0.0553$).

Significant variation in survival rate among source populations was not consistent with local adaptation. Instead, planned contrasts showed that the percentage survival for plants derived from rhizomes collected at the study site (Population 1; 25%) was significantly lower than that of plants from Populations 2 (69%; $P = 0.0044$) and 4 (57%; $P = 0.0492$). The fraction of adults surviving over the winter showed no trend with respect to the elevation or distance from the study site. For example, the two alpine source populations, 1 and 2, had the lowest and highest adult survival, respectively.

ENVIRONMENTAL CONDITIONS IN ESTABLISHED SEEDLING AND ADULT PLOTS

Principal components analysis (PCA) identified three axes of environmental variation that together explained 83.7% of the variance in abiotic parameters among plots (Table 1). Factor 1 exhibited high positive correlations (loadings) with maximum temperature, PAR, and rainfall. Factor 2 was positively correlated with wind speed, and Factor 3 was positively correlated with soil relative water content. Loadings on the first two PCA factors varied significantly among treatments (ANOVA: Factor 1: $F_{4,41} = 58.09$, $P < 0.0001$; Factor 2: $F_{4,41} = 7.08$, $P = 0.002$). Plots in the shade plus wind block treatment resembled plots under willows for both Factors 1 and 2 (Fig. 5). Plots in all other treatments in the open differed significantly from plots in the willow canopy for Factor 1 ($P < 0.015$ for all contrasts). Control and wind block treatments had the highest scores on this axis, indicative of greater

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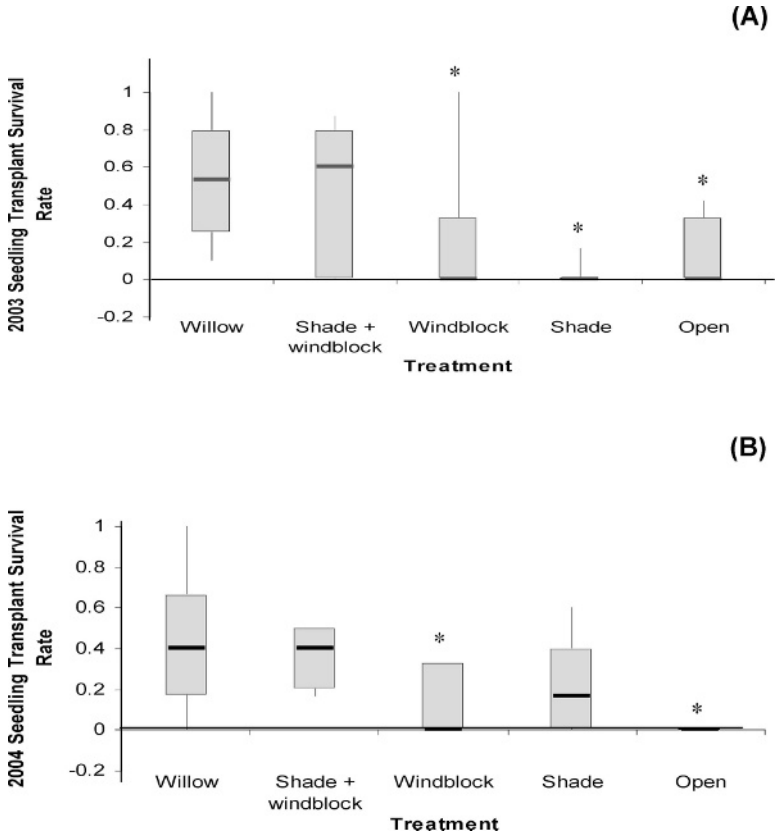


FIGURE 2. Median over-winter survival rate of (A) 2003 and (B) 2004 seedling transplants of *Chamerion angustifolium* placed into experimental microsites (boxes 25–75% quartiles, whiskers 10–90%). Asterisks show treatments differing significantly ($P < 0.05$) from the willow canopy.

maximum temperatures, PAR, and rainfall than in shaded plots or plots under willows. Factor 2 (wind speed) was significantly lower in plots under willows than in open control or shade plots (respectively, $P = 0.0037$ and $P = 0.0026$). However, plots beneath willows had similar loadings on Factor 2 to plots sheltered by wind block ($P > 0.5$; Fig. 5). Factor 3 (soil moisture) did not vary significantly among treatments ($P > 0.2$; Table 1).

Discussion

Results demonstrate that willows promote over-winter survival of established seedling and adult *Chamerion angustifolium* (Figs. 2 and 4). Seed germination and seedling establishment were rare events. Low establishment rates of fireweed have also been observed in low-altitude habitats (56 seedlings from 75,000 seeds sown in the field in Sweden; Broderick, 1990). Since fireweed has no enforced dormancy (Grimes et al., 1988), we conclude that seeds failing to germinate were either dead or had been removed from seed grids by predators, abiotic disturbance, or wind. While seed germination did not statistically differ among treatments, we observed *C. angustifolium* seeds germinating only in shade or canopy environments and establishing only within the willow canopy. We found no evidence that *C. angustifolium* seeds survive over-winter and germinate successfully the following spring in open alpine microsites. Results, while tentative, are consistent with a positive effect of the willow canopy on fireweed recruitment. Because seed planting in this study was timed to coincide with natural seed dispersal of *C. angustifolium* at high elevations, results suggest that fireweed seeds in open alpine microsites are prone to removal over the winter (e.g., by high winds; Chambers and MacMahon, 1994) and/or poor germination and seedling emergence the following summer. Findings from a related experiment in which seeds were planted at snowmelt (early June) to study the impact of drought on alpine fireweed favor the seed loss hypothesis. In that study, patterns of establishment revealed no

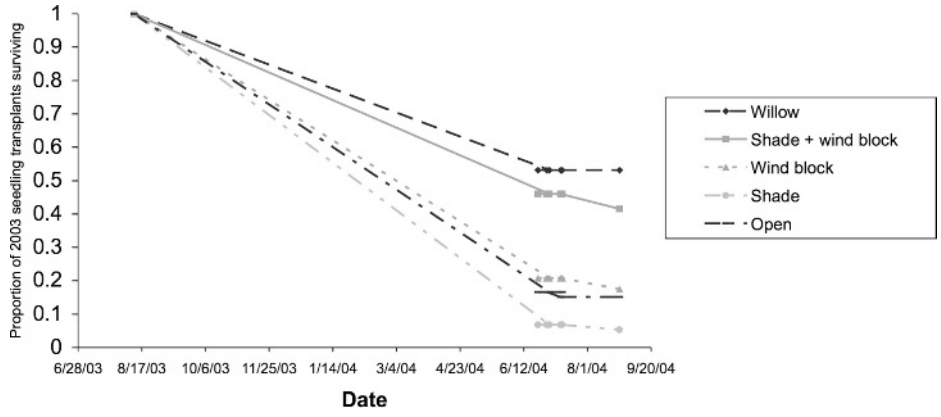


FIGURE 3. Survivorship curves for the 2003 cohort of *Chamerion angustifolium* seedling transplants under each experimental treatment.

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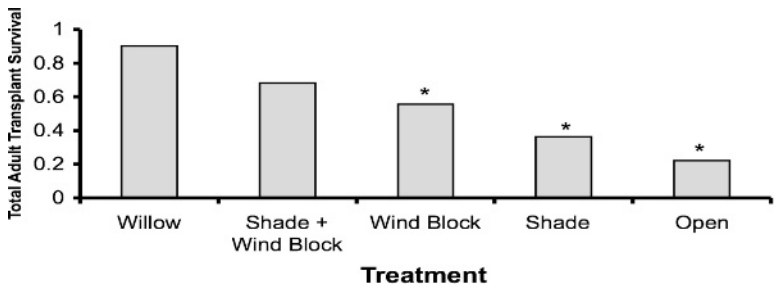


FIGURE 4. Over-winter survival rates for adult transplants of *Chamerion angustifolium* in each treatment. Survival rates are based on pooled plot totals for each treatment group. Asterisks indicate $P < 0.05$ for the difference in survival probability between transplants in open meadow treatments vs. transplants under the willow canopy.

evidence for willow facilitation of establishment under wet or dry conditions (Dona and Galen, 2006).

Protection with shade and wind block mimicked structural components of the willows. PCA results indicated that shade plus wind block treatments captured willow effects on maximum temperature, PAR, rainfall, and wind speed. Established seedlings and adults exhibited similar responses to experimental treatments, with peak survival rates under willows and in the presence of shade plus wind block shelters. Results imply that willows promote fireweed survival over the winter months via synergistic effects of shade and physical shelter. Extreme over-winter mortality in seedlings of *C. angustifolium* contrasts with trends for native alpine plant species (Forbis, 2003). The susceptibility of fireweed to over-winter mortality at seedling (and adult) life history stages may reflect its recent colonization of alpine environments in the central Rocky Mountains coupled with a long evolutionary history in more protected subalpine habitats.

For both seedlings and adults, our statistical ability to detect facilitation was low during the growing season due to the impact of over-winter mortality on plant numbers in exposed plots (Figs. 3 and 4). Consequently, we cannot dismiss the possibility that willows have positive effects on survival and growth of established fireweed during the summer months. Indeed, adult fireweed plants growing within the willow canopy exhibit lower susceptibility to late-season drought than conspecific individuals in the open (Dona and Galen, 2006). Cavieres et al. (2005b) reported similar benefits for herbaceous plant species associated with the nurse cushion plant, *Laretia acaulis*, in the Chilean Andes.

All *C. angustifolium* seedlings surviving over-winter in this study were characterized by aboveground persistence. In all surviving adults, shoots died back in August or September 2003 and new shoots re-emerged in early July 2004 from preformed shoot buds. These results suggest that willows promote both aboveground (leafy tissue) and belowground (root and shoot bud) over-winter survival. Winter alpine stress is dominated by low temperatures and extreme winds. Alpine plants survive over-winter by avoiding exposure to and tissue damage from temperature extremes, or by replacing tissue loss due to exposure (Körner, 2003). In the krummholz, trees and shrubs form islands that protect neighboring herbaceous plants by collecting snow (Carlsson and Callaghan, 1991; Holtmeier and Broll, 1992; Walker et al., 1993). Snow acts as an insulator to reduce temperature fluctuations, frost heave, and water stress to aboveground tissues (Oberbauer and Billlings, 1981; Körner, 2003). This snow fence effect probably accounts for the facilitation of fireweed by alpine willows in our study. Though willows are deciduous, their dense branches provide over-winter shade that in combination with shelter retains snow. After May 2004 and June 2005 storms, snow accumulated and melted more slowly behind wind blocks in shade plus wind block plots and within the willow canopy than in open microsites nearby. These observations are consistent with the idea that increased retention of snow cover by the willow canopy promotes fireweed survival.

In conclusion, our work suggests a "snow-fence" mechanism for commonly observed patterns of association between established seedlings and neighboring shrubby vegetation in the alpine (Billings and Mooney, 1968; Nunez et al., 1999; Niederfringer and Erschambamer, 2000; Cavieres et al., 2002; Arroyo et al., 2003; Castro et al., 2004). By creating sheltered microclimates during the winter, shrubby nurse plants provide herbaceous plants like *C. angustifolium* with opportunities for establishment by seed. After establishment within the willows, *C. angustifolium* may expand into adjacent open areas via vegetative spread. The upward migration of willows and tree species in Sweden and of subalpine tree species in Colorado over the last century has been well documented (Kullman, 2002; Elliot and Barker, 2004). Facilitation between woody shrubs and subalpine herbs may accelerate upward immigration into alpine habitats as global climate change occurs (Parmesan and Yohe, 2003; Arctic Climate Impact Assessment, 2004). Our results underscore the importance of over-winter facilitation, and perhaps more generally snow pack as a potent mechanism for change in alpine plant communities.

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TABLE 1.

Principal components analysis of abiotic conditions in plots containing seedling and adult transplants of *Chamerion angustifolium*. Percent of variance explained by each PCA factor and correlations of abiotic conditions to each factor are given. *P*-values are derived from ANOVA *F*-tests of variation in each PCA factor among treatments. PAR = photosynthetically active radiation, RWC = relative water content.

		Correlations to:					
Factor	% of variance explained	Max. temp.	PAR	Wind speed	Soil RWC	Rainfall	Treatment P
1	42.7	0.83	0.87	0.04	−0.01	0.82	0.0001
2	21.0	−0.09	0.25	0.99	−0.05	0.14	0.0002
3	20.0	−0.05	0.01	−0.05	1.00	−0.05	0.472

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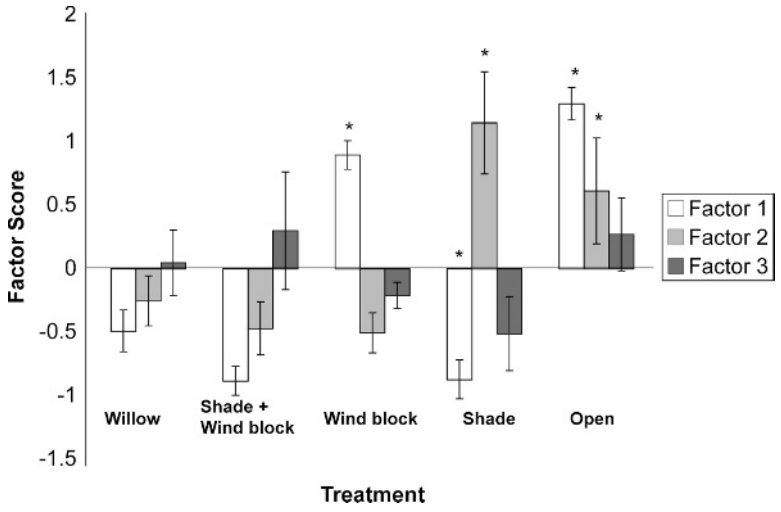


FIGURE 5. Average principal component (Factor) scores (±SE) for plots assigned to different experimental treatments. Asterisks indicate $P < 0.05$ for the difference between average factor scores in each of the open meadow treatments vs. the environment under the willow canopy.

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