Microclimate, freezing tolerance, and cold acclimation along an elevation gradient for seedlings of the Great Basin Desert shrub, *Artemisia tridentata*

Michael E. Loik** & Sean P. Redar†

**Department of Environmental Studies, University of California, Santa Cruz, CA, 95064, U.S.A.
†United States Forest Service, Fawnskin, CA, 92333, U.S.A.

Vegetation, microclimate, seedling frequency, freezing tolerance, and cold acclimation were compared for seedlings of *Artemisia tridentata* collected from 1775, 2175, and 2575 m elevation in the eastern Sierra Nevada, California. Data were used to test the hypothesis that ecotypic differences in stress physiology are important for seedling survival along gradients from desert to montane ecosystems. The vegetation canopy cover and *A. tridentata* seedling frequency were greatest at 2575 m, compared to 1775 and 2175 m. Snow cover ameliorated temperatures near the soil surface for part of the winter and depth varied across elevations. Freezing tolerance was compared for seedlings maintained in growth chambers at day/night air temperatures of 25 °C/15 °C. The temperature at which electrolyte leakage and Photosystem II function (Fv/FM) from leaves were half-maximum was approximately −13.5 °C for leaves of seedlings from all three elevations. Shifting day/night air temperatures from 25 °C/15 °C to 15 °C/5 °C initiated about 1.5 °C of acclimation by plants from all three altitudes, with seedlings from the highest elevation exhibiting the greatest acclimation change. Measurements of ambient air and canopy temperatures at the three elevations indicated that wintertime average low temperatures were consistent with the measured degree of freezing tolerance. At small spatial scales used in this study, pollen and seed dispersal between study sites may have precluded resolution of ecotypic differences. Patterns of freezing tolerance and cold acclimation may depend on a combination of mesoclimate and microclimate temperatures, canopy cover, snow depth, and snow melt patterns.

© 2003 Elsevier Science Ltd.

**Keywords:** air temperature; electrolyte leakage; frost; sagebrush; stress

**Introduction**

Cold is considered one of the most important factors limiting the productivity of plants (Levitt, 1980; Larcher, 1995). Many species are geographically limited by sub-zero temperatures that affect key physiological processes (Levitt, 1980; Nobel, 1988; Loik & Nobel, 1993a). Episodic sub-zero air temperatures (i.e. ‘cold snaps’) are...
common features of the abiotic environment; it is estimated that over half of the Earth’s land mass has a mean minimum temperature below 0°C for some time of the year (Sakai & Larcher, 1987). In cold desert ecosystems sub-zero temperatures can occur near the soil surface based on unstirred boundary layers immediately above the soil surface, radiation of infrared radiation from the surface to a cold nighttime sky, and catabatic cold air drainage (Nobel, 1997). For example, air temperatures 1 cm above the soil surface can be 7° lower than those at 1 m, but dependent on canopy characteristics (Geiger, 1965; Nobel, 1997). Additionally, the temperature near the soil surface exhibits much greater diurnal changes than the mixed air above (Nobel, 1997).

Extreme temperatures can be particularly important for seedling survival and establishment in arid environments. For many ecosystems in the western United States, plant recruitment is limited by the ability of seedlings to survive in the abiotic environment near the soil surface (Franco & Nobel, 1988; Smith & Nowak, 1990). Episodic events of extreme sub-zero air temperatures can contribute to high rates of seedling mortality (Jordan & Nobel, 1979; Fenner, 1985; Sakai & Larcher, 1987). Because seedlings of many species are less tolerant of extreme environmental conditions compared to adults (Smith & Nowak, 1990; Davis & Zabinski, 1992), the degree of abiotic stress tolerance can determine successful establishment and thereby limit species distributions to certain regions or microsites. For example, the elevational and latitudinal distribution of saguaro (Carnegia gigantea) is determined by periods of episodic sub-zero air temperatures (Shreve, 1911; Turnage & Hinckley, 1938; Steenburgh & Lowe, 1983; Nobel, 1988). Indeed, geographic distribution for many desert species is limited by the occurrence of freezing temperatures (Nobel, 1980a, b; Loik & Nobel, 1993a; Pockman & Sperry, 1997; Smith et al., 1997). Franco & Nobel (1989) showed that the microclimate under certain shrubs and grasses reduced the intensity of environmental stress experienced by the desert succulents Ferocactus acanthodes and Agave deserti seedlings. They found strong similarities between the seedling’s temperature tolerance and temperatures experienced within the protective shrub canopy microclimate.

The western limit of the Great Basin Desert is delineated by inland drainage from the Sierra Nevada and Cascade Mountains. Vegetation borders are determined by dispersal ability (Davis & Zabinski, 1992; Clark et al., 1998; Chambers et al., 1999), and recruitment success (Smith & Nowak, 1990; Hoffman & Blows, 1994), which in turn may be restricted by the ability to survive episodic freezing temperatures for certain species (Loik & Nobel, 1993a, b). The purpose of this research was to examine the ecotypic variation in freezing tolerance over an elevation gradient for seedlings of Artemisia tridentata Nutt. (Asteraceae). This species is a widespread evergreen shrub occurring over 7 x 10^6 ha of the Great Basin Desert, it is economically important because cattle will not eat it, and it has exhibited spatial migrations in response to historic climate change (Whitlock & Bartlein, 1993; Nowak et al., 1994). We examined seedlings from the eastern Sierra Nevada of California, where A. tridentata occurs between 1000 and 3500 m (Young et al., 1995). We focused on this species and location because of the potential for dramatic changes in elevational distribution for sagebrush across a wide range of elevations in response to climate change (Nowak et al., 1994). Specifically, we compared membrane and photosynthetic responses to freezing for leaves of A. tridentata seedlings in relation to the thermal microenvironment measured in the field, as well as the tendency for these responses to acclimate following a change in day/night air temperatures in a common garden. We tested the specific hypothesis that A. tridentata seedlings from different elevations exhibit ecotypic differentiation in freezing tolerance and ability to undergo cold acclimation.
Materials and methods

Study sites

Three study sites were located along Bishop Creek, located south-west of Bishop, California (37°22' N latitude, 118°22' W longitude). The bottom of the canyon opens to the north-east and the canyon spans an elevation gradient of 1513 m, from Bishop, California at 1270 m to Lake Sabrina at 2783 m. The canyon is about 19 km long by road, and the study sites were approximately 5 km apart in a north-east to south-west direction. Three research sites were established in or near the canyon spanning an elevation gradient of 800 m. The highest site was located slightly west of Aspendell at 2575 m (37°12' 0''N, 118°35' 23''W), the middle site was located near the Southern California Edison power plant south of California highway 168 at 2175 m (37° 16' 48''N, 118° 32'18''W), and the lowest site was located south-west of Buttermilk Road at 1775 m (37°20' 24''N, 118°31' 14''W). These sites were chosen for elevation and accessibility during winter months.

Climate and microclimate

Weather records from Bishop Municipal Airport, the nearest weather station, were collected from the National Climate Data Center (www.ncdc.noaa.gov), and the Western Regional Climate Center (www.wrcc.sage.dri.edu). Precipitation data were collected for the highest elevation site from the California Department of Water Resources Data Exchange Center (cdec.water.ca.gov).

Air temperatures in the seedling microhabitat were recorded 1 cm above the soil surface using Onset HOBO XT II temperature dataloggers at each site. Measurements were made at 1 h intervals from the fall of 1997 to the spring/summer of 1998. The wire sensors were shielded from direct sunlight and snow by placing them into ventilated opaque plastic vials. The dataloggers were placed in thick plastic bags and buried several centimeters to protect from snow, rodents, and theft. Snow depth was recorded for the three sites on various dates from November 1997 through March 1998.

Species composition and seedling establishment

Three 30 m line transects were randomly located at each site. At 0·3 m intervals, the identity and height of species contacting a 0·25 cm diameter pole were recorded. The relative frequency and coverage was determined using software developed for western North American ecosystems (National Park Service, 1992). The frequency of seedlings of *A. tridentata* occurring at each elevation was determined using detailed searches beneath shrubs within 3 × 30 m belt transects placed adjacent to each line transect.

Plant material

Freezing tolerance and cold acclimation were compared for seedlings grown in a common garden. On November 11, 1997 twenty plants from each elevation were collected for laboratory studies. Small (≤ 10 cm tall) non-reproductive plants were randomly selected and carefully transplanted into conical pots (4 cm diameter × 21 cm tall) filled with soil composed of 1 part potting soil (Supersoil Inc., San Mateo, CA, U.S.A.), 1 part native soil, and 1 part Perlite. The seedlings were watered thoroughly to facilitate transplant survival during transport to the laboratory.
Seedlings were transported to the laboratory within 24 h and placed in a Percival controlled environment chamber at day/night air temperatures of 25°C/15°C, 30% relative humidity, a 12 h/12 h day/night light cycle, and photosynthetically active radiation (PAR; 400–700 nm) of 450 μmol m$^{-2}$s$^{-1}$ on a horizontal surface at the top of the seedlings. Plants were maintained in the growth chamber for a minimum of 30 days before use in experiments to ensure transplant success and acclimation to chamber conditions. To measure the acclimatory change in membrane and photosynthetic susceptibility to freezing temperatures, seedlings were shifted to average day/night air temperatures of 15°C/5°C for 2 weeks before use in experiments (Nobel, 1988; Loik & Nobel, 1993a, b). Air temperatures in the chamber were monitored with Onset HOBO XT II temperature dataloggers. Plants were watered twice per week and fertilized once per week with a 0·1 strength Hoagland’s solution (Hoagland & Arnon, 1950).

**Temperature treatments**

In order to examine tolerance of episodic, low-temperature events (i.e. “cold snaps”), leaves were treated to sub-zero air temperatures after which Photosystem II maximum quantum yield (as $F_V/F_M$) and plasmalemma membrane damage (as electrolyte leakage) were measured. Leaf temperature treatments were performed as described by Loik & Harte (1996) with minor modifications. Low-temperature treatments reaching −5°C were conducted within a modified 0·18 × 0·26 × 0·18 m picnic cooler. Temperatures within the cooler were maintained by placing a 0·18 × 0·18 m heat exchanger connected to a circulating waterbath within the cooler. The waterbath used 60% (v/v) ethylene glycol as the circulated fluid. A small laboratory freezer was used for treatments below −5°C. Temperature in the freezer was regulated by a heat exchanger within the freezer through which warm water was circulated.

Ten leaves per individual were excised and pooled for each of five randomly selected plants per elevation. They were placed in small glass vials for the low-temperature treatment. Temperature treatments started at room air temperature (average 22°C) and decreased at a rate of 3 h$^{-1}$ to the desired temperature (a rate similar to that measured in the field; see also Nobel, 1988). Air temperatures within the chamber or freezer were monitored using a datalogger and 0·5-mm-diameter 30 gauge copper–constantan thermocouples. For leaf temperatures, the thermocouple was woven through the mid-section of the leaf.

Leaves were treated for 1 h at a particular temperature, then warmed at the rate of 3 h$^{-1}$ in the dark until reaching 20°C before being used for chlorophyll a fluorescence ($F_V/F_M$) and electrolyte leakage measurements (described below).

**Electrolyte leakage**

Membrane damage was assessed by electrolyte leakage techniques adapted from Chen et al. (1982) and Loik & Harte (1996). Following low-temperature treatment, a leaf disc was punched from each leaf using a number one cork borer (3 mm diameter). Discs from the same plant, but different leaves, were pooled and placed in separate glass vials with 1·5 ml of distilled water. The discs were then vacuum infiltrated for 5 min to ensure that surface tension would not prevent the exchange of ions from damaged cells to the bathing solution. The vials were then placed on a rotary shaker at 60 cycles min$^{-1}$ for 18–24 h, after which the discs were removed from the bathing solution. The conductivity of the bathing solution was then measured using a Cole Parmer conductivity meter. Between each measurement the probe was rinsed with distilled water and carefully dried with a Kimwipe. Measurements were made for five individuals per site, treatment, and day/night air temperature combination.
Photosystem II responses to freezing

Chlorophyll $a$ fluorescence from Photosystem II (PSII) is a sensitive indicator of biochemical and biophysical susceptibility to low- and high-temperature stresses within chloroplasts (Larcher, 1995). In particular, a decrease in the maximum quantum yield of PSII, $F_v/F_M$, marks the destabilization of chloroplast membranes due to temperature stress (Larcher, 1995; Loik & Harte, 1996; Loik et al., 2000b). After temperature treatments, individual leaves were placed in the sensor head of a Hansatech FMS1 Fluorescence Monitoring System with the following settings: modulated light source set at 3, the pulse light source set at 100, and the actinic light source set at 50. $F_v/F_M$, the maximum quantum yield of Photosystem II, was recorded for one leaf for each of five individuals per elevation, treatment, and day/night air temperature combination.

Statistical analysis

Paired sample $t$-tests were used to determine if air temperatures in the seedling microhabitat were colder for the highest vs. the lowest elevation sites. A single test was performed for a 3·6°C and 5·2°C expected rate of adiabatic cooling between the high- and low-elevation sites because humidity can vary the adiabatic cooling rate (Ahrens, 1991). No comparisons were made between the middle elevation site and the other two sites because of insufficient microclimate data.

Electrolyte leakage and $F_v/F_M$ were plotted against temperature in order to determine LT$_{50}$. LT$_{50}$ is the temperature at which $F_v/F_M$ or electrolyte leakage was 50% of that measured at 20°C and is correlated with whole plant survival for a variety of species (Sakai & Larcher, 1987; Nobel, 1988; Loik et al., 2000b). The average LT$_{50}$ for electrolyte leakage and $F_v/F_M$ for each set of day/night air temperatures were tested for differences between elevation and day/night air temperatures by two-way ANOVA (Zar, 1996). In all statistical tests a sample size of $n = 5$ was used, and $p \leq 0.05$ was considered significant. Statistica (StatSoft, Tulsa, OK) was used to compute all two-way ANOVAs and Excel was used to compute all other statistics.

Results

Climate and microclimate

Monthly maximum and minimum air temperatures, averaged over the period 1961–1990, differed for Bishop (1270 m) and Aspendell (2783 m), the closest recording locations to our study sites (Fig. 1). Maximum air temperatures averaged 38°C in July for Bishop, and 25°C in August for Aspendell. Minimum air temperatures averaged −6°C in January for Bishop, and −10°C in February for Aspendell. Extreme minimum record air temperatures, indicative of episodic cold spells, averaged about −18°C for both Bishop and Aspendell in January. Average annual precipitation for 1961–1990 was 135 mm for the 1775 m site, 313 mm for the 2175 m site, and 422 mm for the 2575 m site.

Snow depth varied by site and date (Fig. 2(A)). All three sites were covered with snow from December into February. Average snow depth was nine-fold greater at the 2575 m site compared to the 2175 m in mid-February, and snow was absent at the 1775 m site by this time. Temperature at 1 cm height above the soil surface was recorded hourly at the upper and lower elevation sites (Fig. 2(B,C)). The lowest recorded temperature of all sites, −13·0°C, occurred at the highest elevation on 16 November, and −9·2°C at the lowest elevation on 3 December.
Species composition and seedling establishment

Four perennial shrub species including *A. tridentata*, *Purshia tridentata* (Pursh) DC (Rosaceae), *Ephedra viridis* Cov. (Ephedraceae), and *Chrysothamnus nauseosus* (Pallas) Britton (Asteraceae) were common at the sites (nomenclature of Hickman, 1993). Herbaceous species included *Lupinus nevadensis* A.A. Heller (Fabaceae), *Eriogonum* sp. (Polygonaceae), and *Erigeron linearis* (Hook.) Piper (Asteraceae). The only tree species on any transect was *Prunus andersonii* Gray (Rosaceae) at the 2175 m site; *Pinus monophylla* Torrey & Fremont (Pinaceae) also occurred near this site, but off the study transects.

Percent cover of plants, litter, rock, and soil varied along the elevation gradient (Table 1). At 1775 m, *E. viridis* was dominant based on cover, whereas at 2175 m *Purshia tridentata* dominated, and at 2575 m, *A. tridentata* was the dominant species. Herbaceous species were more frequent and had greater cover at the highest elevation site compared to the lower sites, and bare ground was more common at the lower two sites. At the high- and middle-elevation sites, ground was covered with more organic litter than at the lowest site. The canopy occupied 44% of samples at 1775 m, 62% at 2175 m, and 76% at 2575 m. Based on three belt transects adjacent to the line transects at each elevation, there were an average of 0.25 *A. tridentata* seedlings m⁻² at 2575 m, and 0.03 seedlings m⁻² at both 1775 and 2175 m.

Freezing tolerance and cold acclimation

Electrolyte leakage for leaves from seedlings grown at day/night air temperatures of 25°C/15°C increased for discs from leaves exposed to treatment temperatures below −12.5°C (Fig. 3). The temperature leading to half-maximum electrolyte leakage (LT₅₀) was calculated based on these patterns. For seedlings maintained at day/night air temperatures of 25°C/15°C, LT₅₀ was −13.3°C for plants from 1775 m, −13.4°C for 2175 m, and −13.9°C at 2575 m. Following a shift to day/night air temperatures of 15°C/5°C, LT₅₀ was −15.1°C, −15.2°C, and −14.2°C for the 1775, 2175, and 2575 m sites, respectively (Fig. 3). Based on electrolyte leakage for seedlings grown at the two day/night air temperature regimes, and treated at −12°C, a significant degree of acclimation occurred (Table 2), but there were no differences in LT₅₀ based on elevation differences (p = 0.106).

For leaves from seedlings grown at day/night air temperatures of 25°C/15°C, Fᵥ/Fₘ markedly decreased following treatment at temperatures between −12.5°C and −17.5°C (Fig. 4). This response was similar for seedlings from all three elevations, as well as for seedlings 2 weeks following a shift to day/night air temperatures of 15°C/
C. A 50% reduction in $F_v/F_M$ for seedlings grown at 25°C/15°C resulted from treatment at temperatures from −14.1°C to −15.1°C across the three elevations. The effects of growth at different day/night temperatures were significant only for seedlings from the 2175 m site, but site and growth temperature did not significantly affect $F_v/F_M$ in the overall ANOVA model.

**Discussion**

For seedlings of *A. tridentata* from three sites along the 800 m elevation gradient maintained at day/night air temperatures of 25°C/15°C, and then shifted to 15°C/5°C,
results for electrolyte leakage indicate acclimation by 1.5°C, but no differences across elevations. Moreover, there were no significant differences across sites or growth temperatures for chlorophyll \(a\) fluorescence from PSII. Freezing tolerance, based on \(LT_{50}\) values for freezing tolerance measured in the laboratory, is close to the minimum microclimate temperatures recorded at the 2575 m site during the course of this study. Moreover, the temperature leading to a 50% reduction in membrane integrity and chlorophyll \(a\) fluorescence was 11°C lower than the 1961–1990 average minimum air temperatures for Bishop in February, but 5°C higher than the extreme minima for the same period. Together, these results suggest that seedlings have a “safety buffer” or difference between the temperature leading to a 50% loss in membrane structure and function, and the air temperatures recorded during the study. Based on the 1961–1990 record, extreme minimum temperature events as low as \(-18°C\) would represent important filters on recruitment, at least in terms of membrane damage and PSII function.

Electrolyte leakage measurements suggest a 1.5°C acclimation response by the seedlings, especially for those from the 1775 and 2575 m sites. With regard to the effects of freezing temperatures on Photosystem II function, chlorophyll fluorescence indicates a shift in \(F_v/F_M\) of 0.6° only for seedlings from 2575 m. Differences in \(F_v/F_M\) from PSII would indicate variation in susceptibility of the photosynthetic apparatus to low temperatures (Berry & Bjorkman, 1980; Larcher, 1995). The lack of differences across sites and growth temperatures suggests a limited ability of the photosynthetic apparatus to acclimate or evolve ecotypic differences, at least at the spatial scale of site comparisons in the present study. Differences in membrane susceptibility following a shift to lower growth temperatures could be beneficial for seedling survival as temperature extremes, snow cover, and other aspects of the microenvironment vary over short temporal scales. Variation within populations for cold acclimation has been demonstrated for many other species (Smithberg & Weiser, 1968; Green, 1969; Maronek & Flint, 1974; Eiga & Sakai, 1984; Loik & Nobel, 1993a). However, in these other studies differences in cold tolerance were found in plants from regions spanning broad elevation and latitudinal gradients whereas in the present study the greatest geographic range between sites was about 5 km, and 800 m in elevation. Freezing tolerance for Artemisia skorniakowi and A. pamirica from the arid East Pamir Mountains was similar to our results for A. tridentata (Tyurina, 1957). However, these
values were based on measurements for summer frost hardiness which could be higher than those determined after winter acclimation. Also, our results are based on seedlings maintained at 25°C/15°C and 15°C/5°C, and acclimation might have been greater (and LT₅₀ lower) for plants if the day/night temperatures of the chambers could have been set lower than 15°C/5°C. A different photoperiod within growth chambers compared to natural populations may also affect the degree of cold acclimation (Howe et al., 1995; Rinne et al., 1998).

Microclimatic effects could complicate patterns of variation in freezing tolerance for S. tridentata over the 800 m of our elevation gradient. Plants at higher elevations may avoid low temperatures beneath the snow pack, while

![Figure 3](image-url)

**Figure 3.** Electrolyte leakage as a function of treatment air temperature for seedlings of *Artemisia tridentata* from 2575 m (A), 2175 m (B), and 1775 m (C). Data are means ± 1 S.E. (n = 5) for plants maintained at day/night air temperatures of 25°C/15°C (●) or 14 days after shifting to 15°C/5°C (▲).
exposed plants at lower elevations experience low temperatures within their tolerance range. Thus, selection for cold tolerance may be based on microclimate at small scales. Moreover, other stresses, such as drought and high-temperature stress, as well as wind-blown ice, snow, and dust, can also reduce seedling survival (Tranquillini, 1979; Baskin & Baskin, 1998). Also, PSII responses to freezing temperatures can be complicated by high PFD, which has been shown to affect recruitment in seedlings of other species (Ball et al., 1997; Egerton et al., 2000). Given the broad distribution of *A. tridentata* across North America, differences among populations in the ability to tolerate freezing would seem likely when compared across larger scales. In this regard, Meyer et al. (1990) found that seed germination response variables for *A. tridentata* were correlated with the mean January temperatures at various seed collection sites. For *A. tridentata*, pollen and seeds are dispersed by wind (Shultz, 1993), so the potential for the mixing of pollen and seed from high and low elevations is likely at the spatial scale of our comparisons. In the eastern Sierra Nevada cold air in the high mountains descends downslope, frequently generating strong winds. During the autumn, when *A. tridentata* is flowering, cold fronts generate strong northerly winds, while differential surface heating in the Owens Valley and other nearby valleys can generate strong southerly winds (Hidy & Klieforth, 1990). Combined, high rates of pollen and seed dispersal may reduce the potential for differentiation between populations from higher and lower elevations (Nowak et al., 1994).

Low-temperature tolerance changes little throughout the year for certain species because episodic freezing can occur at high altitudes even during summer months (Sakai & Larcher, 1987). It is not uncommon for freezing temperatures, even snow storms, to occur in the eastern Sierra Nevada during the summer months (Anderson, 1975). However, woody temperate zone shrub species, especially those spanning broad gradients like *A. tridentata*, usually have some ability to acclimate to low temperatures. Cold acclimation is most common for species from regions with high-temperature seasonality (Sakai & Larcher, 1987; Alberdi & Corcuera, 1991). In the present study lowering of the growth chamber’s day/night air temperature regime was used to trigger an acclimation response. The small magnitude of response by plants to the lowering of day/night air temperatures may indicate that *A. tridentata* seedlings require greater decreases in day/night temperatures to enhance their acclimation response. Such is the case with cacti and agaves (Nobel, 1988). Furthermore, it is possible that lowering air temperature alone was insufficient to initiate an acclimation response intense enough to be measured by the techniques employed. For many species, different or additional environmental cues are needed to stimulate a robust acclimation response. A decrease in photoperiod is important for the acclimation of many woody shrubs, conifers, and northern tree species, but is not as important for herbaceous species (Sakai & Larcher, 1987). In some cases, a combination of short days and colder temperatures is required for cold acclimation (Alberdi & Corcuera, 1991). Seedlings of *A. tridentata* may require a greater decrease in day/night air

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Electrolyte leakage</th>
<th>$F_{\text{V}}/F_{\text{M}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>0.106</td>
<td>0.626</td>
</tr>
<tr>
<td>Growth temperature</td>
<td>6.992*</td>
<td>0.042</td>
</tr>
<tr>
<td>Site × growth temperature</td>
<td>1.031</td>
<td>2.393</td>
</tr>
</tbody>
</table>

Data are $F$ values, for $n = 5$ plants per elevation site or growth temperature; *$p<0.05$.|

Table 2. Summary of two-way ANOVA results for LT$_{50}$ for membranes (as determined by electrolyte leakage) or Photosystem II function (as determined by measurements of $F_{\text{V}}/F_{\text{M}}$) following temperature treatment in the laboratory.
temperatures and a decrease in photoperiod to significantly increase the acclimation response.

The microclimate data suggest that the minimum low temperatures experienced between the 1775 and 2575 m sites differed by several degrees. Between those two sites a difference of 3.6–5.2°C was expected based on the adiabatic lapse rate (4.5–6.5°C per 1000 m depending on water content), and the actual value was 4.1°C. Temperature fluctuations and low-temperature extremes were not as low when snow depths were greater at the 2575 m compared to 1775 and 2175 m sites. During these times,

Figure 4. Photosystem II maximum quantum yield (measured as $F_v/F_m$) as a function of treatment air temperature for seedlings of Artemisia tridentata from 2575 m (A), 2175 m (B), and 1775 m (C). Data are means ± 1 S.E. ($n = 5$) for plants maintained at day/night air temperatures of 25°C/15°C (●) or 14 days after shifting to 15°C/5°C (▲).
temperatures near the soil surface remained at approximately 0°C. These results are consistent with studies in the Rocky Mountains and Canada (Gieger, 1965). Despite being 800 m lower than the highest elevation site, temperatures at the 1775 m site were lower when there was less insulating snow cover. Adults and seedlings of *A. tridentata* at the 2575 m site were completely snow covered for the majority of the winter, and intermittently covered at the 1775 and 2175 m sites. Seedling survival at high altitudes may depend on sufficient snow cover to ameliorate low temperatures near the soil surface.

The vegetation formed a more complete canopy at the highest elevation study site. The shrub crowns tended to touch one another, leaving only small openings in the canopy. The *A. tridentata* seedlings tended to occur under the canopy, whereas at the lower elevation sites they were more exposed. This could influence seedling survival, especially at the higher elevation because temperatures in the microclimate near the soil surface depend, in part, upon IR flux from surrounding vegetation and litter (Nobel, 1997). The large amount of bare ground without organic litter at the lowest elevation site could lead to lower than expected temperatures near the soil surface due to a large IR flux at night, when the ground loses heat to the atmosphere (Gieger, 1965; Nobel, 1997). The vegetation canopy may also serve to protect seedlings from ice encasement and snow pressure.

The mechanisms by which plants have responded to past changes in climate depended, in part, on how physical factors influenced seedling establishment (Clark *et al*., 1998). Insights into seedling tolerances to abiotic factors may help our understanding of how future changes in climate will impact the distribution and productivity of vegetation. The future climate of the Sierra Nevada may include increased summer monsoon rainfall (Knox, 1991; Arritt *et al*., 2000), which could enhance seedling recruitment for certain species. Experimental warming that changes soil water content in the Rocky Mountains alters water relations, photosynthesis, and above-ground biomass accumulation for various species (Harte & Shaw, 1995; Loik & Harte, 1997; Loik *et al*., 2000a), impacting tolerance of temperature extremes (Loik & Harte, 1996), and seedling recruitment. The effects of changing climatic features (i.e. temperature and precipitation) on plant fitness parameters, such as seedling recruitment and adult reproductive effort, require further experimentation along gradients from high-elevation desert to montane ecosystems.

References


Y uok, M. E. & S. P. REDAR