Dependence of winter water relations of mature high-elevation *Picea engelmannii* and *Abies lasiocarpa* on summer climate

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Summary  Water relations of Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) trees growing at an elevation of 3230 m on Mt. Evans, Colorado, USA, were studied during the winters of 1995–1996 and 1996–1997. During both winters, current-year and 1-year-old shoots were collected weekly and their relative water contents (RWC) determined. Measured meteorological parameters were used in a conifer winter water relations model, WINWAT, to simulate changes in shoot RWC of *P. engelmannii* and *A. lasiocarpa* during the winter. The model failed to predict shoot RWCs in 1996–1997 when calibrated with 1995–1996 data. The cold early summer of 1995 inhibited xylem formation, which appears to have caused lower rates of water recharge to the needles during the 1995–1996 winter than during the 1996–1997 winter. We conclude that summer climate strongly affects winter water relations in these subalpine species, and that changes in both summer and winter climate must be considered when predicting future ranges of these species.

Keywords: modeling, conifers, Colorado, Front Range, Rocky Mountains.

Introduction

Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are dominant species in the upper part of the subalpine forests of Colorado, USA (Peet 1988). Winters in this region are characterized by low temperatures, strong winds and prolonged exposure to snow. Water loss occurs by cuticular transpiration despite presumed stomatal closure during the winter (Boyce et al. 1991b, 1992). The availability of water to replace these losses may be limited, because frozen soil or air embolisms in the xylem can hinder water transport to the needles (Havranek and Tranquillini 1995). Therefore, maintaining an adequate foliar water supply during winter is crucial for the survival of subalpine conifers (Tranquillini 1979).

Several early studies reported that, at high elevations and high latitudes, conifer root water uptake is cut off in winter (Hygen 1965, Wardle 1968, Lindsay 1971). Nevertheless, winter recharge must occur because the total amount of water lost through transpiration is several times greater than the initial water content of needles at the onset of winter (Hygen 1965, Boyce et al. 1991b). Boyce and Lucero (1999) observed root water uptake by *P. engelmannii* saplings during the winter. However, the main source of water for needle recharge in mature trees is the stem (Waring and Running 1978, Grace 1990, Boyce et al. 1991b, 1992, Sowell et al. 1996). Sowell et al. (1996) showed that severed shoots of *P. engelmannii* in Colorado desiccated more quickly than attached shoots, indicating that stem water was used by intact shoots during the winter. The freezing point of xylem water in some evergreens is depressed to between –2 and –6 °C (Tranquillini and Holzer 1958, Havis 1971, Lipp and Nilsen 1997). Temperatures exceed –4 °C for significant periods during winter in subalpine forests in Colorado (Boyce et al. 1991b, 1992). However, freezing and subsequent thawing of xylem tissue can create air embolisms, or cavitations, that can drastically reduce xylem transport (Hygen 1965, Tyree and Sperry 1989, Havranek and Tranquillini 1995). Havis (1971) suggested that refilling of cavitated tracheids or vessel elements is not necessary for winter water transport, because cell wall pores, or micropores, can conduct a significant amount of water. However, Robson and Petty (1993) showed that micropore transport alone is insufficient to meet the winter transpiration needs of conifers, and they proposed mechanisms by which cavitation could be reversed during warm periods in the winter to permit water movement through the lumen.

Water content of needles during winter is determined by a balance between recharge and transpiration and is strongly correlated with needle viability, which declines significantly at relative water contents (RWC) near 60% (Tranquillini and Holzer 1958, Havis 1971, Lipp and Nilsen 1997). A short, cool growing season can cause incomplete cuticle development, leading to increased needle desiccation and mortality (Grace and van Gardingen 1996).

Winter water relations of high-elevation *P. rubens* Sarg. in New Hampshire, USA, were previously modeled by WINWAT, and the results indicated that water lost from foliage was replaced by stored reserves in the stem (Boyce et al. 1991b, 1992). The purpose of the present study was to determine if WINWAT can also be used to model winter water relations of current-year and 1-year-old shoots of high-elevation
P. engelmannii and A. lasiocarpa in the Rocky Mountains of Colorado.

Materials and methods

Study site

The study site was located at the University of Denver’s High Altitude Laboratory on Mt. Evans, Colorado (39°40′ N, 105°35′ W), at an elevation of 3230 m. The site is dominated by Picea engelmannii and Abies lasiocarpa, with scattered individuals of Pinus contorta Dougl. Snow covered the area during the study periods of both the winters of 1995–1996 and 1996–1997 (Table 1). Because data presented here were collected after January 1 of each winter, these winters are referred to as 1996 and 1997, respectively.

Field measurements

A 10-m meteorological instrument tower was erected at the site in fall 1995. The data used for this study were recorded from January 26, 1996 to May 5, 1996 and from January 22, 1997 to March 28, 1997. Instrumentation on and near the tower measured air, soil and conifer needle temperature, relative humidity, total irradiance, wind speed and direction, and soil water potential (Table 1). Measurements were taken every minute, and mean, maximum and minimum values were calculated and recorded every hour with a CR-10 data logger (Campbell Scientific, Inc., Logan, UT). Needle temperature was measured on one P. engelmannii and one A. lasiocarpa tree. Type T (copper-constantan) thermocouples, constructed out of 40-gauge wire and soldered into loops that would fit over needles (Boyce et al. 1992), were installed in the mid-crown on the south side of each tree. Thermocouples

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>$T_a^1$</th>
<th>$T_l^2$</th>
<th>$T_s^3$</th>
<th>RH$^4$</th>
<th>SI$^5$</th>
<th>WP$^6$</th>
<th>WS$^7$</th>
<th>WD$^8$</th>
<th>SN$^9$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>Jan (745)</td>
<td>–7.8 (–22.0, 8.0)</td>
<td>–11.9 (–22.2, 5.6)</td>
<td>–2.6 (–4.4, –1.7)</td>
<td>54.6 (9.8, 92.1)</td>
<td>768 nw</td>
<td>2.4 (0.2, 11.2)</td>
<td>245.1 (55.9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Feb (696)</td>
<td>–5.3 (–26.7, 6.4)</td>
<td>–5.2 (–28.4, 21.0)</td>
<td>–2.6 (–3.4, –1.8)</td>
<td>48.0 (5.8, 97.7)</td>
<td>1014 nw</td>
<td>2.1 (0.2, 8.9)</td>
<td>243.1 (58.0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mar (744)</td>
<td>–5.1 (–22.7, 10.3)</td>
<td>–4.8 (–24.2, 25.4)</td>
<td>–1.5 (–3.4, –0.1)</td>
<td>52.9 (8.8, 95.4)</td>
<td>1300 &lt; –1, –0.06</td>
<td>1.7 (0.2, 9.7)</td>
<td>235.4 (66.0)</td>
<td></td>
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<tr>
<td></td>
<td>Apr (720)</td>
<td>–1.6 (–14.9, 13.5)</td>
<td>–2.5 (–23.1, 30.5)</td>
<td>–0.2 (–0.4, –0.1)</td>
<td>55.3 (13.1, 96.7)</td>
<td>1348 &lt; –1, –0.03</td>
<td>1.9 (0.2, 10.7)</td>
<td>238.8 (68.7)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>May (728)</td>
<td>5.7 (–3.7, 18.1)</td>
<td>6.0 (–4.9, 37.4)</td>
<td>3.2 (–0.1, 13.4)</td>
<td>54.9 (12.1, 100)</td>
<td>1472 &lt;0.04, –0.03</td>
<td>1.4 (0.2, 7.8)</td>
<td>215.2 (83.5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>Jan (419)</td>
<td>–5.1 (–19.8, 6.8)</td>
<td>–4.8 (–22.7, 25.7)</td>
<td>–2.6 (–3.2, –1.8)</td>
<td>48.1 (8.2, 94.0)</td>
<td>775 nw</td>
<td>2.2 (0.2, 8.4)</td>
<td>255.9 (37.9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Feb (672)</td>
<td>–9.1 (–21.1, 5.9)</td>
<td>–8.6 (–22.4, 21.2)</td>
<td>–2.7 (–3.4, –1.8)</td>
<td>63.1 (13.0, 95.2)</td>
<td>976 nw</td>
<td>1.2 (0.2, 9.3)</td>
<td>204.4 (84.2)</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Mar (744)</td>
<td>–2.1 (–17.9, 12.2)</td>
<td>–1.6 (–18.7, 27.8)</td>
<td>–1.1 (–2.3, 0.1)</td>
<td>41.1 (7.6, 95.6)</td>
<td>1157 &lt; –1, –0.04</td>
<td>1.9 (0.2, 9.9)</td>
<td>251.0 (53.3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Apr (720)</td>
<td>–4.5 (–25.0, 11.3)</td>
<td>–4.0 (–25.7, 29.6)</td>
<td>0.0 (–0.1, 0.1)</td>
<td>66.7 (11.0, 99.7)</td>
<td>1370 &lt; –1, –0.03</td>
<td>1.5 (0.2, 7.8)</td>
<td>208.2 (90.5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>May (744)</td>
<td>3.4 (–10.9, 17.8)</td>
<td>3.8 (–11.7, 28.3)</td>
<td>1.6 (0.0, 13.1)</td>
<td>60.3 (10.4, 100)</td>
<td>1355 &lt;0.10, –0.03</td>
<td>1.3 (0.2, 7.0)</td>
<td>228.3 (76.6)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Number of hourly measurements taken in that month in parenthesis. Note that January 1997 data collection began on January 14.
2 Air temperature (°C) at 10 m: means, with minima and maxima in parenthesis.
3 Leaf temperature (°C) from one spruce and one fir tree: means, with minima and maxima in parenthesis.
4 Soil temperature (°C) at 5 cm: means, with minima and maxima in parenthesis.
5 Relative humidity (%) at 10 m: means, with minima and maxima in parenthesis.
6 Solar irradiance (W m−2): maxima only.
7 Soil water potential (MPa) at 5 cm: minima and maxima. nw = months when frozen soils prevented proper probe function.
8 Wind speed (m s−1) at 10 m: means, with minima and maxima in parenthesis. Stall speed of the anemometer is 0.2 m s−1 and is thus the lowest speed recorded.
9 Unit mean vector wind direction (°): mean and standard deviation.
10 Maximum snow depth (cm), with number of days with snow depth ≥ 2.5 cm in parenthesis; na = missing data.
were placed on two needles per species and per needle age class (current-year and 1-year-old), for a total of four thermocouples per species. Additional thermocouples were installed as replacements for those that failed.

Each week, from January 12, 1996 to May 18, 1996 and from January 22, 1997 to March 28, 1997, shoots were removed from four *P. engelmannii* and four *A. lasiocarpa* trees (not the trees with installed thermocouples). Different sets of four *P. engelmannii* and four *A. lasiocarpa* trees were used for each year of study to minimize effects of excessive upper-canopy removal. Ranges of diameter at breast height (DBH) and tree height were 21.1–36.5 cm and 11.1–18.0 m, respectively, for *P. engelmannii*, and 14.9–22.3 cm and 9.8–15.0 m, respectively, for *A. lasiocarpa*. One branch containing sun foliage was collected with the aid of a telescopic pole pruner from opposite sides of each tree (a total of two branches per tree). Foliage was kept in sealed plastic bags over ice in darkness during transport to the laboratory. Four current-year and 1-year-old shoots were randomly excised from the two branches per tree and weighed (fresh mass). Fresh mass was determined within 4 h after collection. Shoots were then fully hydrated by floating on deionized water for 24 h at approximately 4 °C in the dark. Hydrated shoots were blotted dry and reweighed (turgid mass). Shoots were then oven-dried at 60 °C for 3 days and weighed again (dry mass). Shoot relative water content (RWC; %) was computed as:

\[
RWC = \frac{m_f - m_d}{m_i - m_d} \times 100, \quad (1)
\]

where \(m_f\), \(m_d\), and \(m_i\) are fresh, dry, and turgid masses, respectively (Koide et al. 1991). Mean RWC and 95% confidence intervals for each date, species and age class were computed from the mean relative water contents of each tree.

On February 4, 1996 and March 19, 1997, the same shoots used for RWC measurements were also used to determine foliar cuticular conductances by a modification of the method described by Herrick and Friedland (1991) and Boyce et al. (1991b, 1992). After determination of shoot turgid mass, shoots were placed in a dark chamber maintained at 4 °C and 20% relative humidity. Temperature and relative humidity were monitored and recorded with a temperature/relative humidity probe (Model CS500, Campbell Scientific, Inc.) and data logger. The shoots were weighed at approximately 12-h intervals for 3 days, and then oven-dried and weighed. Leaf surface area was estimated from a dry mass–surface area relationship developed for mature trees at this site (R.L. Boyce, unpublished data). Data for the first 24-h period were discarded because of possible stomatal transpiration. Additional details are given in the Appendix.

**Model structure**

The WINWAT model (Figure 1) is a modification of the model described by Boyce et al. (1992). The single state variable in the model is the water content of a representative shoot per unit leaf area (WC; g m⁻²) and is equal to shoot fresh mass

\[
WC = \frac{m_f - m_d}{m_i - m_d} \times 100, \quad (2)
\]

where \(L\) is shoot leaf area (m²). The denominator was derived from a fit of turgid to dry masses by a linear regression line with zero intercept \((m_f = am_d)\) and a linear regression with zero intercept of leaf area on shoot dry mass \((L = bm_d)\). Thus, the denominator in Equation 2 reduces to \((a - 1)/b\).

If stomata are assumed to remain closed during the winter (Marchand and Chabot 1978), transpiration is directly proportional to the difference in water vapor density between the air spaces in the needle interior and the atmosphere, whereas it is inversely proportional to the sum of the cuticular and boundary layer resistances (Sowell 1985). Because boundary layer resistance is usually about three orders of magnitude less than cuticular resistance, it was ignored. For this study, we used cuticular conductance, which is the inverse of cuticular resistance. Transpiration rate \((T; \text{g H}_2\text{O m}^{-2} \text{day}^{-1})\) in WINWAT was expressed as:

\[
T = (\Delta \rho_{\text{H}_2\text{O}}) g_e, \quad (3)
\]
where $\Delta \rho_{\text{air}}$ is difference in water vapor density (g H$_2$O m$^{-3}$) between the needle interior ($\rho_{\text{in}}$) and the atmosphere ($\rho_{\text{atm}}$), and $g_c$ is cuticular conductance (m day$^{-1}$). The form of cuticular conductance expressed in Equation A10 in the Appendix was used for $g_c$.

Atmospheric water vapor density ($\rho_{\text{atm}}$) was set equal to the saturation water vapor density for the measured air temperature, multiplied by the relative humidity (expressed as a fraction). The value of $\rho_{\text{atm}}$ was the saturation vapor density for the measured temperature of the needle, because the internal relative humidity of the needle air spaces was assumed to be 100% (Fitter and Hay 1987). Saturation vapor densities at different temperatures were taken from tabulated values (List 1984).

It was assumed that shoots are connected to a reservoir of water available in the stem (Boyce et al. 1991b, 1992). Water flux through the stem is proportional to its water potential (Tranquillini and Holzer 1958, Havis 1971, Saugier et al. 1997), $T_{\text{air}} > T_{\text{th}} = -4 ^\circ C$. When $T_{\text{air}} > T_{\text{th}}$, $R = 0$ at RWC = 100%, $R = R_p$ at RWC = 0%, and $R = 0.1 R_p$ at RWC = 90%. Based on the original model calibration (Boyce et al. 1991b, 1992) and published data (Tranquillini and Holzer 1958, Havis 1971, Saugier et al. 1997), $T_{\text{th}}$ was set to $-4 ^\circ C$.

Hourly means of air and needle temperatures and relative humidity were used as driving variables in the model. Shoot water content per unit leaf area at time $i$ was calculated as:

$$WC_i = WC_{i-1} + (R_i - T_i)dt,$$  

where $WC_{i-1}$ is shoot water content per leaf area at time $i-1$ (g m$^{-2}$), $R_i$ is recharge rate at time $i$ (g H$_2$O m$^{-2}$ day$^{-1}$), $T_i$ is transpiration rate at time $i$ (g H$_2$O m$^{-3}$ day$^{-1}$) and $dt$ is time step (day). A time step of 0.02 days (about 30 min) was used (cf. Boyce et al. 1991b, 1992). Because parameters were measured every hour, their values for the time steps falling between measurements were estimated by linear interpolation. A fourth-order Runge-Kutta simulation algorithm was employed (HPS 1994). Equation 2 was used to convert WC to RWC.

**Model calibration and validation**

The 1996 measurements were used to calibrate the recharge parameter $R_p$ in Equation 4. The RWCs measured on January 26, 1996 were used to set initial values during model calibration. WINWAT was run for the four combinations of species and foliage age classes with the appropriate values of measured needle temperature, cuticular conductance and measured water content as inputs. The model was run with variations of $R_p$ until the sum of squares between modeled and measured RWCs was minimized. The 95% confidence interval of this minimum sum of squares was estimated by the accelerated bootstrap procedure recommended by Dixon (1993). A fourth-order polynomial was then fit to estimate the sum of squares as a function of $R_p$. The intersections of the polynomial with the upper 95% confidence limit of the minimum sum of squares were used to estimate the upper and lower 95% confidence limits of the estimated value of $R_p$.

The 1997 data were used to validate the model, and RWCs measured on January 22, 1997 were used to initialize the model. Meteorological data and cuticular conductances measured in 1997 and $R_p$ calibrated with 1996 measurements were used for each species and age class. Because $R_p$ calibrated with the 1996 measurements predicted 1997 RWCs so poorly, $R_p$ was recalibrated with data from 1997 and then used to predict 1997 RWCs.

**Transpiration estimates**

Data were available from both winters from day of year 26.42 to 87.58. We used meteorological data, measured cuticular conductance, and Equation 3 to estimate mean transpiration rates of each species and age class combination for this period in both years.

**Results**

**Measured RWC and $g_c$**

Measured RWC varied between 84 and 92% for current-year *Picea engelmannii* and *Abies lasiocarpa* shoots and between 74 and 85% for 1-year-old shoots during the 1996 winter (Figure 2). During the 1997 winter, measured RWC of both species varied between 85 and 91% for current-year shoots and 86 and 87% for 1-year-old shoots (Figure 3). In both years and species, RWC was consistently lower in 1-year-old shoots than in current-year shoots. Measured RWCs were significantly higher in 1997 than in 1996, except for current-year shoots of *A. lasiocarpa* (Table 2).

Mean cuticular conductances at RWC = 100% are shown in Table 3. There were no statistically significant differences in $g_c$ between years except for current-year shoots of *A. lasiocarpa*, where $g_c$ was higher in 1997 than in 1996. However, there was no overlap between years in the range of $g_c$ calculated by WINWAT for any of the species or age classes. In most cases, the range of modeled $g_c$ was higher in 1997 than in 1996, except for 1-year-old shoots of *A. lasiocarpa*.

**Model calibration**

In 1996, $R_p$ values were 50 and 65 g m$^{-2}$ day$^{-1}$ for current-year and 1-year-old shoots of *P. engelmannii*, respectively, and the corresponding values for *A. lasiocarpa* were 55 and 170 g m$^{-2}$ day$^{-1}$ (Figure 2, Table 4). When these 1996 $R_p$ values were used to calibrate WINWAT, the predicted RWCs for 1997 generally fell below the 95% confidence intervals of the measured values (Figure 3), except for 1-year-old shoots of *A. lasiocarpa*. When WINWAT was recalibrated with $R_p$ values
for 1997, much better fits between measured and modeled RWCs were obtained (Figure 3). For current-year shoots of *A. lasiocarpa*, all modeled RWCs fell within the 95% confidence interval of measured RWCs when $R_p$ was set to 95 g m$^{-2}$ day$^{-1}$. The other fits were not as good, but best results were obtained when $R_p$ was set to 150, 105 and 210 g m$^{-2}$ day$^{-1}$ for 1-year-old shoots of *A. lasiocarpa* and current-year and 1-year-old shoots of *P. engelmannii*, respectively. In most cases, 1997 RWCs were larger than 1996 RWCs; however, the 95% confidence intervals for the two winters did not overlap, except for 1-year-old shoots of *A. lasiocarpa* (Table 4).

**Transpiration estimates**

With the exception of 1-year-old shoots of *A. lasiocarpa*, estimated transpiration rates were higher in 1997 than in 1996 (Table 5). This difference was associated mainly with a greater estimated mean $\Delta \rho_{HO2}$ in 1997 than in 1996. These transpiration rates are also estimates of mean recharge rates, because initial and final RWCs in each winter were similar.

**Discussion**

Despite statistically significant differences, measured RWC for the same age class and species did not vary greatly between the winters of 1996 and 1997. However, modeled RWCs for 1997, based on the recharge parameter $R_p$ calibrated from 1996 data, were underestimated in all cases. Thus, factors associated with the physiology of the trees must have changed between the two years, and these changes were not initially accounted for in the model. This year-to-year difference in $R_p$ was not observed in a previous application of the model in New Hampshire, where WINWAT calibrated with an $R_p$ value derived from measurements of current-year shoots in winter 1990 accurately predicted RWC of current-year shoots in winter 1991 (Boyce et al. 1992). WINWAT is sensitive to changes in cuticular conductance or resistance (Boyce et al. 1991b); however, this source of error was ruled out by determining conductance in both years. Although conductance was only measured once per winter, studies of conifers in New England have shown that $g_c$ varies little in most winters (Boyce et al. 1992, Vostral 1999).

To determine why WINWAT performed poorly in 1997, we examined the underlying assumptions of the model; i.e., that stomata remain closed during the winter and that water uptake by roots is limited or nonexistent. Sowell et al. (1996) reported that there was no stomatal opening in timberline *Picea*
engelmannii in Colorado in winter 1994, and the soil remained frozen during most of the 1996 and 1997 winters at our site at Mt. Evans (Boyce and Lucero 1999). Because different trees were sampled in each year, it is possible that less vigorous trees were chosen in 1996; however, this appears unlikely because RWC, gc, and Rp generally moved in similar directions from 1996 to 1997 for all species and age classes.

June and July 1995 were significantly colder than June and July 1996 in much of Colorado. Because June 1996 temperatures at the Mt. Evans weather station, which is ~100 m from our site, were unavailable, summer 1995 and 1996 temperatures from several other high-elevation sites in Colorado were examined (Table 6). The most comparable data are from Leadville (39°14’ N, 106°18’ W), at an elevation of 3063 m (Table 6). June and July temperatures were lower in 1995 than in 1996 at all of the sites shown in Table 6. At Leadville, June and July temperatures were both 2.0 °C lower in 1995 than in 1996. The temperature at Mt. Evans was 1.4 °C lower in July 1995 than in July 1996. These lower summer temperatures were associated with the formation of smaller tree rings (Table 7), which correspond to differences in recharge parameters between the winters of 1996 and 1997. Although the tree ring data were collected at breast height (1.37 m), ring-width trends similar to those found at breast height are likely to occur in twigs and branches, where water is being transported from

Table 2. Mean measured RWC between days of the year 20 and 90 during the winters of 1996 and 1997 (January 1 = day of year 1). Standard deviations are shown in parenthesis (n = 9). P-Values refer to results of t-tests.

<table>
<thead>
<tr>
<th>Species</th>
<th>Needle age</th>
<th>Mean RWC</th>
<th>1996</th>
<th>1997</th>
<th>P</th>
</tr>
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<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>P. engelmannii</td>
<td>Current-year</td>
<td>87.49</td>
<td>88.42</td>
<td>&lt; 0.005</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.24)</td>
<td>(1.78)</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>One-year-old</td>
<td>80.44</td>
<td>83.52</td>
<td>&lt; 0.001</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>(1.82)</td>
<td>(2.81)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. lasiocarpa</td>
<td>Current-year</td>
<td>88.87</td>
<td>88.78</td>
<td>&gt; 0.50</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.03)</td>
<td>(1.07)</td>
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<tr>
<td></td>
<td>One-year-old</td>
<td>81.67</td>
<td>82.99</td>
<td>&lt; 0.01</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>(2.87)</td>
<td>(1.70)</td>
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</table>

Figure 3. Measured and modeled relative water contents (RWC) of (A) current-year and (B) 1-year-old shoots of P. engelmannii and (C) current-year and (D) 1-year-old shoots of A. lasiocarpa during winter 1997. Error bars are 95% confidence intervals. Calibrated values of Rp are shown in the legend and in Table 4.
sapwood to foliage, because cambial growth propagates from the shoot tips downward (Kozlowski et al. 1991). Current-year foliage is supplied only by wood formed in the previous summer, whereas 1-year-old foliage is supplied by wood formed in the last two summers. At lower temperatures, photosynthate can be converted to sugars and starch, rather than to cellulose, which is a component of cell walls (Tranquillini 1979). A delay in the onset of summer can cause a delay in the formation of wood early in the season, which usually comprises a larger fraction of the tree ring than wood formed late in the season (Kozlowski 1991). Therefore, inadequate xylem wall formation in the summer of 1995 may have resulted in low recharge rates during the winter of 1996, especially for current-year shoots.

Because low summer temperatures and inadequate xylem cell wall formation are usually associated with poor needle cuticle formation (Tranquillini 1979), we expected to see higher values of $g_c$ in 1996 than in 1997. However, $g_c$ of current-year shoots, which should have been more sensitive to temperatures of the previous summer, were higher in 1997 than in 1996, and significantly so for Abies lasiocarpa (Table 3).

Wood formation, particularly of early wood, occurs well before the commencement of bud break and shoot growth in conifers (Tranquillini 1979). Cuticular formation, however, continues throughout the growing season (Lange and Schulze 1966, Tenberge 1992). Because mean temperatures were 1.1 °C higher in August 1995 than in August 1996 at both Mt. Evans and Leadville (Table 6), it is possible that the higher temperature in August 1995 allowed cuticles to mature longer,
leading to lower $g_c$ in winter 1996 than in winter 1997.

The study site is approximately 300 m below the alpine timberline. Trees at this site showed none of the symptoms of winter stress noted in other studies (e.g., Tranquillini 1979, Hadley and Smith 1983, 1986). Nonetheless, the modeled winter recharge rates appeared to be sensitive to changes in summer temperatures. Although it is possible that the WINWAT model is faulty, we note that WINWAT worked fairly accurately, was greater in 1997 than in 1996, indicating that mean recharge must also be greater in 1997 than in 1996. Thus, the model findings are supported by both the data on tree ring widths and estimated transpiration rates.

Measured $g_c$ was consistently higher in 1-year-old foliage than in current-year foliage (Table 3). Similar findings have been reported for other conifers in winter (Vostral 1999). The increase in $g_c$ with needle age may be associated with the progressive degradation of epicuticular waxes, as has been observed in *Picea rubens* and *Abies balsamea* (L.) Carr. (Boyce et al. 1991a).

When variations in $R_w$ between years are taken into account, WINWAT predicts RWC fluctuations well. In New Hampshire, modeled RWC declined when relative humidity fell below 60% (Boyce et al. 1991b). In Colorado, relative humidity was frequently below 60% and sometimes below 10% (Table 1); however, modeled declines in RWC were not associated with low humidity but with temperatures below $-4 \, ^\circ\text{C}$ (data not shown). For example, modeled declines in RWC were observed on Days 25–35 and 55–65 in 1996 (Figure 1) and on Days 35–40 and 50–60 in 1997 (Figure 2). Thus, factors that reduce recharge are predicted to be more important for winter water relations in Colorado, whereas factors that increase transpiration are more important in New Hampshire.

Meteorological data from this region of Colorado indicate that the summer climate has become cooler and wetter (Stohlgren et al. 1998), and conifer seedlings are establishing at lower elevations. We conclude that cooler summers will decrease xylem and cuticle formation, causing more winter water stress and forcing subalpine conifers to lower elevations. On the other hand, humidity in this region has increased since 1973 (Ross and Elliott 1996), even in winter. If this trend continues, subalpine conifers should experience less stress in winter. Thus, although tree line may be depressed by summer climate, elevational ranges of subalpine conifers may increase.

### Table 6. Monthly mean temperatures for the summers of 1995 and 1996 at sites in Colorado near Mt. Evans. Data are from the Colorado Climate Center (http://ccc.atmos.colostate.edu).

<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation (m)</th>
<th>Year</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>June</td>
</tr>
<tr>
<td>Aspen</td>
<td>2487</td>
<td>1995</td>
<td>12.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>14.2</td>
</tr>
<tr>
<td>Evergreen</td>
<td>2134</td>
<td>1995</td>
<td>13.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>15.8</td>
</tr>
<tr>
<td>Georgetown</td>
<td>2612</td>
<td>1995</td>
<td>11.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>14.1</td>
</tr>
<tr>
<td>Grant</td>
<td>2649</td>
<td>1995</td>
<td>10.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>13.7</td>
</tr>
<tr>
<td>Leadville</td>
<td>3063</td>
<td>1995</td>
<td>8.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>10.1</td>
</tr>
<tr>
<td>Mt. Evans</td>
<td>3240</td>
<td>1995</td>
<td>5.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>–</td>
</tr>
<tr>
<td>Vail</td>
<td>2507</td>
<td>1995</td>
<td>10.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1996</td>
<td>11.8</td>
</tr>
</tbody>
</table>

By 1996 the model findings are supported by both the data on tree ring widths and estimated transpiration rates.

### Acknowledgments

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### References


### Appendix

According to Cape and Percy (1996), the mass of a detached leaf (or, for conifers, a detached shoot) drying under constant conditions is:

\[
m(t) - m_{\infty} = (m^{*} - m_{\infty})e^{-kt},
\]

where \(m(t)\) is the mass at time \(t\), \(m_{\infty}\) is the equilibrium mass, \(m^{*}\) is the extrapolated mass back to \(t = 0\) that would have occurred had all water vapor been lost only through the cuticle, and \(k\) is a decay constant with units of time\(^{-1}\). The equilibrium

---


mass $m_\infty$ is approximately equal to $m_d$. Thus, water content is given as:

$$WC(t) = WC_0 e^{-kt},$$  \hspace{1cm} (A2)

where $WC(t)$ is the water content at time $t$ and $WC_0$ is the turgid water content.

Cuticular conductance ($g_c; \text{m s}^{-1}$) is determined as:

$$g_c = \frac{T}{\Delta\rho_{H_2O}},$$  \hspace{1cm} (A3)

where $T$ is transpiration rate (g m$^{-2}$ s$^{-1}$), and $\Delta\rho_{H_2O}$ is the vapor density difference between air inside the leaf and outside the boundary layer (g m$^{-3}$). Transpiration ($T$) may be expressed as:

$$T = \frac{dWC}{dt},$$  \hspace{1cm} (A4)

where $L$ = surface area of the leaf (m$^2$). Thus, $dWC/dt$ will decrease with decreasing water content. Substituting Equation A2 into Equation A4 yields:

$$\frac{dWC}{dt} = \frac{d(WC_0 e^{-kt})}{dt} = -kWC_0 e^{-kt}.$$  \hspace{1cm} (A5)

Thus, ignoring the minus sign,

$$T = \frac{kWC_0 e^{-kt}}{L},$$  \hspace{1cm} (A7)

and, from Equation A3,

$$g_c = \frac{kWC_0 e^{-kt}}{L(\Delta\rho_{H_2O})}.$$  

Relative water content (RWC; expressed as a fraction) is given as:

$$RWC(t) = \frac{WC(t)}{WC_0}. $$  \hspace{1cm} (A8)

From Equation A2:

$$RWC(t) = \frac{WC_0 e^{-kt}}{WC_0} = e^{-kt}.$$  \hspace{1cm} (A9)

Thus, substituting Equation A9 into Equation A7,

$$g_c = \frac{k(WC_0)(RWC)}{L(\Delta\rho_{H_2O})} = g_{c_0} RWC,$$  \hspace{1cm} (A10)

where $g_{c_0} = \frac{kWC_0}{L(\Delta\rho_{H_2O})}$ is the cuticular conductance at full turgor ($RWC = 1$ or 100%). Cuticular conductance therefore declines linearly with decreasing RWC, as found by Hadley and Smith (1990). Decay constants $k$ were calculated from exponential curve fits to drying curves for each shoot ($r^2$ values usually exceeded 0.99). The value of $WC_0$ was determined as the difference between turgid and oven-dry masses of each shoot. Mean $\Delta\rho_{H_2O}$ was calculated from measured temperatures and relative humidity and tabulated values of vapor saturation density (List 1984), where air inside the leaf was assumed to be saturated.