Water Relations of Selected Plant Species in the Alpine Tundra, Colorado

James R. Ehleringer, Philip C. Miller

Ecology, Volume 56, Issue 2 (Early Spring, 1975), 370-380.

WATER RELATIONS OF SELECTED PLANT SPECIES IN THE ALPINE TUNDRA, COLORADO[1]

JAMES R. EHLERINGER[2] AND PHILIP C. MILLER

Department of Biology, San Diego State University, San Diego, California 92182 USA

Abstract. The purpose of this study was to measure some aspects of the water relations of selected plant species in the alpine tundra, Colorado, in order to assess the possible role of water limitation on primary production. Leaf water potentials were measured in *Kobresia myosuroides, Geum rossii, Bistorta bistortoides, Deschampsia caespitosa,* and *Caltha leptosepela.* Leaf resistances to water loss were measured in *Bistorta* and *Caltha.* Measurements were made at dawn and midday throughout the season and several times through selected days in plants along a moisture gradient. Leaf resistance was related to leaf water potential, light, and temperature. Leaf water potentials decreased throughout the season and were higher on the wetter site. Minimum water potentials of the species in the order listed above were −40, −23, −17, −31, and −17 bars. Minimum leaf resistances of *Bistorta* and *Caltha* were 0.8 and 1.6 s · cm^{-1}, respectively, and were lower on the wetter site. Both *Bistorta* and *Caltha* on the wet meadow showed partial midday stomatal closure, but *Bistorta* on the dry meadow did not. At −16 bars leaf resistance increased abruptly in *Caltha,* but was still low in *Bistorta.* Leaf resistances were low at incident solar radiation levels of 0.2 ly · min^{-1} and at temperatures near 20°C. Leaf resistances increased with temperatures below 15°–20°C. Root resistances for *Bistorta* were 0.9 × 10^4 s · cm^{-1} · bar^{-1} at the dry site and 0.8 × 10^4 at the wet site, and for *Caltha* were 0.6 × 10^4 s · cm^{-1} · bar^{-1} at the wet site. The changing daily pattern of leaf water potential and leaf resistance is shown to be related to the diurnal environmental pattern, to root resistances, and to the relationships between leaf resistance and leaf water potential and between leaf water potential and leaf relative saturation deficit.

Key words: Alpine tundra; leaf resistances; leaf water potential; plant distribution; plant water relations; primary production; soil–plant–atmosphere system; water stress.

INTRODUCTION

The purpose of this study was to measure some aspects of the water relations of selected plant species in the alpine tundra meadow on Niwot Ridge, Colorado, in the context of water movement through the soil–plant–atmosphere system, in order to assess the possible role of water limitation on primary production. At low leaf water potentials, water limitation of production may occur by stomatal closure restricting water loss and photosynthesis or by reduced growth due to decreased cell turgor. Only the stomatal changes are considered here. Cox (1933) suggested that production in the alpine tundra may be limited by the length of the growing season, low temperatures, and moisture. Billings and Bliss (1959) showed that soil moisture and production were correlated in an alpine snowbank in Wyoming and that production was affected by short periods of drought even though soil water potentials were above −15 bars. Soil moisture determinations by Bliss (1956) in the top 12.5 cm of soil indicated water potentials below −15 bars in 67% of the observations on the ridgetop, in 45% on the north-facing slope, and in 25% on the south-facing slope. For European alpine

tundra, Tranquillini (1963, 1964) stated that plant water stress occurs mainly during the winter when the soils are frozen and water lost from leaves cannot be replaced, and occurs rarely during the summer. Kuramoto and Bliss (1970) reported that, in the subalpine communities of the Olympic Mountains in Washington, leaf water potentials were similar among different species in dry grass–forb, mesic grass, and *Saussaurea* moist forb communities; but that net photosynthesis of several species decreased as soil water potential decreased. For several alpine and subalpine species, Anderson and McNaughton (1973) observed that relative leaf water content and growth were reduced by soil cooling, whereas net photosynthesis and transpiration were not affected. Anderson (1971) also found plants from moist habitats to have higher transpiration and photosynthetic rates than those from dry habitats. In the Sierra Nevada alpine, Mooney et al. (1965) found that species from moist sites transpired more than species from dry sites and transpiration of plants from moist sites decreased during midday, but transpiration of plants from dry sites remained constant throughout the day. Scott and Billings (1964) and Hillier (1970) considered soil moisture as a principal factor limiting plant growth in the alpine.

Plant water stress may develop from low soil moisture or strong evaporative demands because of

high radiation intensities and large vapor density gradients. On Niwot Ridge a drought period of several weeks occurs early in the season until convectional storms supply moisture to the soil (Osburn 1958, Marr 1967). Even with rains, the high radiation intensities and high evapotranspiration rates may cause a net loss of moisture from the soil. Bliss (1956) concluded that the environment in the alpine tundra had higher winds, large vapor density gradients, higher solar radiation loads, and lower soil moisture than that in the arctic. In the alpine, Salisbury and Spomer (1964) measured temperatures more than 20°C above ambient. Temperatures of cushion plants departed more from air temperature than did those of erect plants. These large temperature differences imply large vapor density gradients between the leaf and the air and strong transpirational demands. If water uptake is less than transpiration, leaf water stress may develop and stomates may close.

The plant water relations are viewed in a simple model of the soil–plant–atmosphere continuum. Differences in water potentials between the leaf and soil provide the driving force for water absorption across root and soil resistances. Water loss from the leaf is related to a difference in vapor densities of leaf and air and is impeded by the resistance of the leaf, including stomates and cuticle, and leaf air boundary layer. The leaf resistance varies with the leaf water potential to control the rate of water loss and maintain the leaf water content. The model is essentially that of Honert (1948), modified by Rawlins (1963) and described in nonmathematical terms by Jarvis and Jarvis (1963). It is intended to provide a dynamic, interpretive framework for viewing leaf water potentials. It requires measurements of the relations between leaf resistance and leaf water potential and between leaf water potential and leaf water content, and of root and soil resistance, in addition to the relations of leaf resistance to solar radiation and leaf temperature, and the daily course of these environmental variables.

DESCRIPTION OF SITE

The study was conducted on Niwot Ridge in the Front Range in central Colorado (40° 02′ N, 105° 33′ W). The surface of the ridge is between 3,300 and 3,800 m altitude and is gently rolling along an east–west axis with several distinct knolls forming high points along its length. In the meadows, an organic horizon of undecomposed and partially decomposed plant material sometimes extends from the surface to about 5 cm, below which occurs a stony loam that hardens when it becomes dry (Osburn 1958).

Data on the climate at 3,048 and 3,750 m have been tabulated by Marr et al. (1968) and analyzed by Barry (1973). The climate of the area is generally continental. Winds are predominantly westerly and strong with peak velocities above $45 \text{ m} \cdot \text{s}^{-1}$ in winter. From June through August mean velocities are $5–7 \text{ m} \cdot \text{s}^{-1}$. Mean maximum temperatures are above freezing from May to October and between 8° and 13°C in the summer. Mean minimum temperatures are above freezing from June through August. Precipitation averages about 1,000 mm annually, with 25% occurring in the summer. Precipitation on the Ridge is low in May and June and high in July; convectional storms usually occur in July and August. During the summer of 1972, when these measurements were made, precipitation did not begin until late July.

METHODS

The area chosen for the study is at 3,500 m elevation and is approximately 1 km wide, bordered on the east and west by two knolls. Five sites were chosen along a moisture gradient (Fig. 1). Site 1, the driest and most exposed to wind, was in fellfield tundra on the east knoll of the Saddle in vegetation consisting predominantly of *Silene acaulis* L. and *Kobresia myosuroides* (Vill.) Fiori. Site 2 was in an area dominated by *Kobresia* between sites 1 and 3. Site 3 was exposed to prevailing winds and kept snow-free throughout the winter. It contained a diversity of species, including *Geum rossii* (R. Br.) Ser., *Bistorta bistortoides* (Pursh) Small, and *Deschampsia caespitosa* (L.) Beauv. Site 4 occupied the center of a trough between sites 3 and 5 and was dominated by *Salix nivalis* Hook. Site 5, the wettest and most protected from the prevailing winds, was covered by snow during the winter and received meltwater from snow until the end of June. Vegetation at site 5 consisted primarily of *G. rossii*, *B. bistortoides*, *D. caespitosa*, *Caltha leptosepela* D.C., and *Artemesia scopulorum* Gray. Taxa studied were *Kobresia*, *Geum*, *Bistorta*, *Deschampsia*, and *Caltha*. *Kobresia* occurred only on sites 1, 2, and 3; *Geum* and *Bistorta* on all sites; *Deschampsia* on sites 3, 4, and 5; and *Caltha* on sites 4 and 5. Measurements were also taken near a mobile instrument van in an area similar in species composition, topography, and elevation to site 3, and in another area similar to site 5 which included *Caltha*. Nomenclature follows Weber (1967).

Air temperatures and relative humidity were measured in a Stevenson screen with a hygrothermograph, and solar radiation was measured with a pyrheliograph by the Institute of Arctic and Alpine Research through the summer. On July 2, 8–9, and 16–17 and August 2–3, 10–11, and 21–22 microclimatic measurements were made. Total and diffuse

Fig. 1. View of the study sites on Niwot Ridge, looking east across the Saddle in late July. This area in the foreground was under snow until June 27. The instrument shelters and mobile van can be seen.

solar radiation was measured with Moll-Gorzynski solarimeters, net radiation with a Fritchen net radiometer, soil heat flux with three Thornthwaite heat flux discs, air and soil temperatures with shielded 24-gauge copper-constantan thermocouples, vapor densities with a dew point hygrometer, and wind profiles with a Thornthwaite wind register system. Rain was measured with four rain gauges, one pair at each end of the transect. The mean of the four gauges is presented.

Leaf water potential was measured with a pressure bomb (PMS Instrument Co., Corvallis, Oregon). Both N_2 and compressed air were used, depending on the availability of each gas, but N_2 was used when available. A comparison of values using N_2 and air showed no difference in measured values. Leaf water potentials of the five species were measured every 2 wk between June 15 and August 22 and every 3 h throughout the day at sites 3 and 5 on June 30, July 22, August 10–11, and August 21–22. Water potentials of four leaves from each species at a site were measured each time.

Leaf resistance to water loss was measured on attached leaves with a porometer (Kanemasu et al.

1969). Because of the size of the aperture on the porometer only broad leaves could be measured; therefore, resistances were measured only on Bistorta and Caltha. The porometer and the leaf were shaded to equalize temperatures between the porometer sensor and the leaf surface. Ambient air temperatures were measured concurrently to the nearest degree Celsius with a shaded thermistor (Yellow Springs Instrument, Yellow Springs, Ohio). The porometer was calibrated in the mobile van at 3,500 m using Plexiglas plates with different-sized holes (Kanemasu et al. 1969). Calibrations were performed at several temperatures covering the range experienced in the field (5°–20°C) to correct for the temperature effects on the porometer sensor (Morrow and Slatyer 1971). Resistances were measured independently for the upper and lower leaf surfaces and were calculated as the mean of the parallel resistances of the upper and lower surfaces. Leaf resistances were measured every 3 h on July 5 and 19 on sites 1 through 5, and in the morning (0600–0900 h) and one or two times later in the day every 7 days from July 5 to August 9 on sites 3 and 5. Resistances of four leaves were measured each time.

Relative saturation deficit (RSD) was measured by excising leaves and taking ¼-in. (0.635-cm) diameter punches from a leaf. The punches were weighed immediately to measure their fresh weight. It frequently required 1–2 min from excision until the leaf discs could be punched and weighed in the mobile van. The leaf discs were floated on distilled water for 60 min at room temperature, and then reweighed to measure their turgid weight. On June 15 water uptake curves were measured for samples of three leaves of all species except *Caltha* by reweighing repeatedly through a 2½-h period. After 40 min no further weight gain was measured. Relative saturation deficit was calculated as the turgid weight minus the fresh weight divided by the turgid weight, and expressed as a percent.

We determined the relationship between leaf resistance and leaf water potential by measuring resistances and water potentials on groups of five leaves randomly selected from 1-m² quadrats on sites 3 and 5 and near the van. Means were calculated from five measurements. Measurements were taken only under high light intensities. *Bistorta* were chosen from sites 3 and 5 and near the van and *Caltha* from site 5 and near the van. The relationship between leaf water potential and RSD was determined for *Bistorta* and *Caltha* near the van and checked with data taken from sites 3 and 5. With *Bistorta* on site 3, *Caltha* and *Bistorta* near the van, the water potential of one leaf of a pair was measured while the other leaf was carried to the van to measure the RSD. With *Caltha* on site 5, because of the distance from the van, the water potentials of four leaves adjacent to each other were measured while four other leaves were brought back to the mobile lab in a shaded glass vial. The means of each group of four measurements were used to calculate the RSD of *Caltha*.

The relationships between leaf resistance and light intensity, and between leaf resistance and leaf temperature were measured near the mobile van with a Sieman's gas exchange system (Koch et al. 1971). Two cambridge dew point hygrometers (Model 880, E. G. and G. International Inc., Waltham, Massachusetts) tracked incoming (ambient) and outgoing water vapor contents. Leaf temperatures were measured with 40-gauge copper-constantan thermocouples threaded through the leaves. All sensors were coupled to a data acquisition system with on-line processing (Vidar Corp., Mountain View, California). Leaf resistances were measured at several levels of temperature and irradiation. The temperature response was measured at 5°C increments from 10° and 35°C with full sun irradiation. The light response was measured at three or four intensities with leaf temperatures at 10°C.

RESULTS

Climate and microclimate

On June 6, half of site 5 was covered with snow and the other half with meltwater. All the snow and meltwater had disappeared by July 27. The other sites were free of snow and meltwater from June 6 on. On July 7, 4.0 mm of precipitation fell and on July 20, 4.5 mm, with only traces of precipitation on three other days. After July 20 precipitation increased. Between July 21 and 31, 15.5 mm fell and between August 1 and 20, 37.9 mm. Typically in July and August the sky was clear in the morning, cloudy at noon, and clear in late afternoon. Daily solar radiation was highest in late June and July and decreased in August because of the cloudiness and lowered solar altitude. Diffuse solar radiation was 7%–8% of the total solar radiation on clear mornings and increased throughout the day to 100% under clouds. The albedo of the vegetation was 0.19 throughout the season under clear and cloudy skies. Throughout the season long-wave radiation averaged $0.37 \text{ cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$ with clear skies and 0.42 under cloudy skies. Winds were usually from the west at $3–20 \text{ m} \cdot \text{s}^{-1}$. Wind during July and August was usually higher in the morning than in the afternoon. Wind speeds measured at five heights between 20 and 320 cm at different times in the season showed a logarithmic profile with a roughness parameter of 1.66 cm over a community comprised of *Kobresia, Geum, Bistorta,* and *Deschampsia.* Maximum air temperatures in the screen increased while minimum temperatures showed no trend throughout the season. Air temperatures in the canopy 1 cm above the soil were up to 16°C warmer during the day and 8°C cooler at night than air temperatures at 10 or 80 cm above the surface. Soil surface temperatures were similar to canopy air temperatures during the night and varied between 0.2° and 27.6°C. Soil temperatures of −5 cm depth ranged between 5° and 10°C. Minimum relative humidities correlated with maximum air temperatures. Maximum relative humidities often indicated unsaturated air at night. Vapor density differences between 20 and 4 cm heights were commonly $1 \text{ g} \cdot \text{m}^{-3}$ and occasionally $2 \text{ g} \cdot \text{m}^{-3}$. Vapor densities at 20 cm were constant throughout the day and ranged from 3.3 to $7.2 \text{ g} \cdot \text{m}^{-3}$ throughout the season, increasing slightly as the season progressed. Vapor densities at 4 cm varied between $3.4 \text{ g} \cdot \text{m}^{-3}$ and $9.1 \text{ g} \cdot \text{m}^{-3}$.

Leaf water potentials

Dawn (0530–0730 h) and midday (1100–1400 h) leaf water potentials in all five species tended to decrease throughout the season (Fig. 2). On site 3, dawn water potentials of *Kobresia* increased follow-
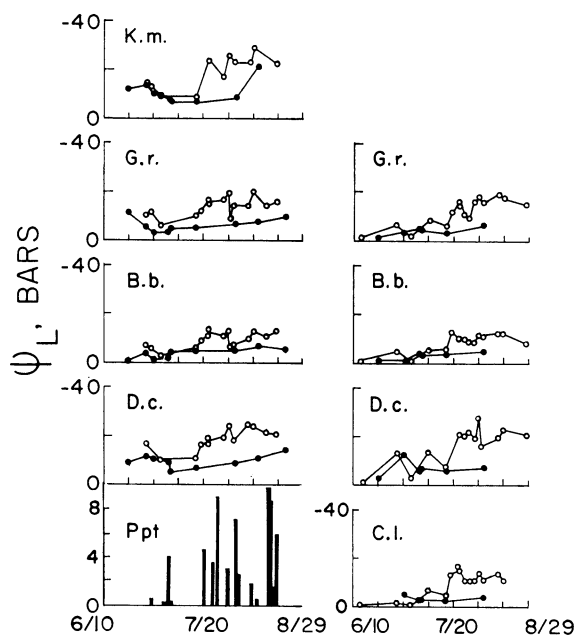
FIG. 2. Seasonal courses of dawn (●) and midday
(○) leaf water potentials (Ψ_L) in *Kobresia myosuroides*
(K.m.), *Geum rossii* (G.r.), *Bistorta bistortoides* (B.b.),
Deschampsia caespitosa (D.c.), and *Caltha leptosepela*
(C.l.). Left column, water potentials from site 3; right
column, from site 5. Daily precipitation (Ppt) in milli-
meters is given for both sites.

FIG. 3. Daily courses of leaf water potentials (Ψ_L)
of five species on June 30 (○) and July 22 (●). Species
symbols are the same as in Fig. 2. Left column, water
potentials from site 3; right column, from site 5.

ing the July 6 rain and remained between −6 and −9
bars until August. On August 11, a water potential
in *Kobresia* of −22 bars occurred (mean of four
measurements) before sunrise, which was 12 bars
lower than *Deschampsia* and 15 bars lower than
Geum and *Bistorta* at the same time. Dawn water
potentials of *Geum* on site 3 decreased from −3 to
−10 bars and those of *Bistorta* from −1 to −6 bars.
Dawn water potentials of *Deschampsia* rose from
−11 in late June to −5 bars following rain on July 6,
then declined to −14 bars. On site 5, dawn water
potentials of *Geum* decreased from −1 to −7 bars;
those of *Bistorta* from −1 to −5 bars; those of *Des-
champsia* from −3 to −7 bars and those of *Caltha*
from −2 to −4 bars.

On sites 3 and 5 dawn leaf water potentials of
Kobresia were lower than those of *Deschampsia* on
site 3, while *Deschampsia* was lower than the other
species on sites 3 and 5. *Geum* was lower than *Bis-
torta*, which was lower than *Caltha*. These differences
may reflect differences in rates of nighttime tran-
spiration, in root depth and soil water potential in
the root zone, or in the root and soil system resis-
tances. While meltwater was present on site 5, dawn
water potentials were higher there than on site 3.
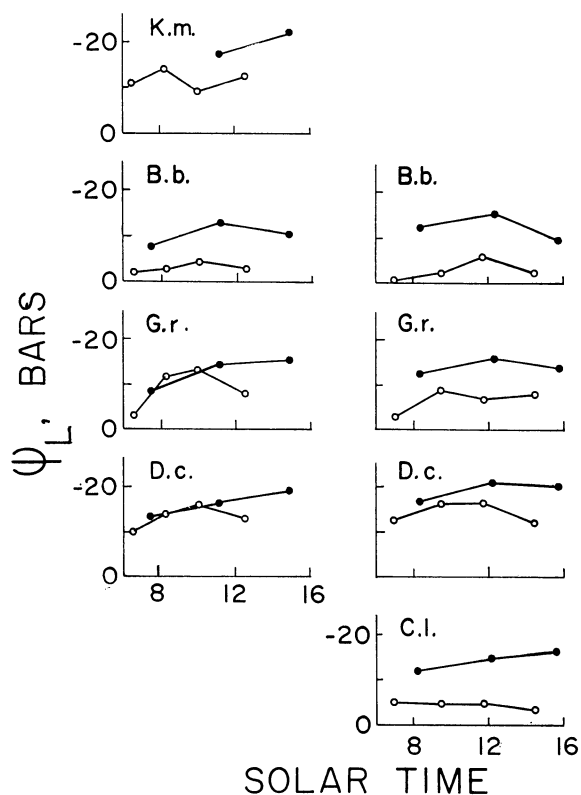After the meltwater ceased, dawn water potentials
were similar on sites 3 and 5.

The midday leaf water potentials decreased
throughout the season, but were more variable than
the dawn water potentials because of variations in
the midday weather conditions (Fig. 2). On site 3
midday leaf water potentials of *Kobresia* decreased
from −12 to about −30 bars, with −40 bars measured
on August 11 near the van; those of *Geum* decreased
from −12 to −20 bars; those of *Bistorta* from −4 to
−17 bars; and those of *Deschampsia* from −17 to
−25, with −31 bars measured on July 29. On July 6
and 10, which were cloudy and cooler than the pre-
vious days, leaf water potentials were higher than
the previous measurements. On site 5, throughout
the season, midday leaf water potentials decreased
from −3 to −20 bars for *Geum*; from −2 to −12 bars
for *Bistorta*; from −2 to −24 bars for *Deschampsia*;
and from −2 to −16 bars for *Caltha*. As meltwater
disappeared from site 5, *Deschampsia* leaf water po-
tentials decreased rapidly. Leaf water potentials of
the other species decreased more gradually. The
midday leaf water potentials were usually lower on
site 3 than on site 5, especially while there was melt-
water on site 5. After the meltwater ceased on site
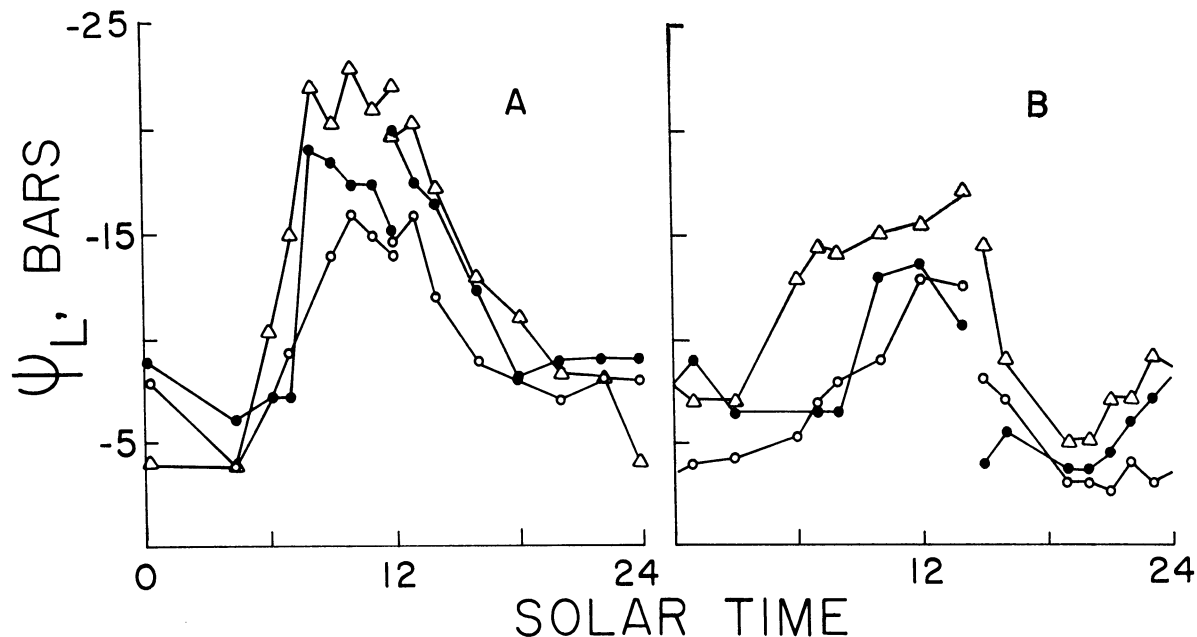5, these differences between sites 3 and 5 diminished.

FIG. 4.   Daily courses of leaf water potentials (Ψ_L) of *Geum* (●), *Bistorta* (○), and *Deschampsia* (△) on August 10–11 (A) and August 21–22 (B).

Although midday leaf water potentials of *Geum* showed no consistent difference between sites 3 and 5, those of *Bistorta* were almost 3 bars lower and those of *Deschampsia* 2–5 bars lower on site 3 than on site 5 throughout the season. The lowest leaf water potentials measured were −40, −23, −17, and −31 bars for *Kobresia, Geum, Bistorta,* and *Deschampsia* on site 3 and −20, −12, −24, and −17 bars for *Geum, Bistorta, Deschampsia,* and *Caltha* on site 5. Mean water potentials in Fig. 2 are somewhat higher.

Not only did the magnitude of the leaf water potentials change, but the pattern of water potentials throughout the day also changed (Fig. 3). On June 30 the general pattern on both sites was for leaf water potentials to decrease to a minimum value between 1000 and 1300 h solar time, then to increase. However, *Caltha* remained low throughout the day. On July 22, before the summer rain began, leaf water potentials of *Geum* on site 5, *Bistorta* on sites 3 and 5, and *Caltha* on site 5 were lower than on June 30 by 5 to 10 bars. Leaf water potentials of *Deschampsia* were slightly lower. Potentials of all species decreased in the morning. *Bistorta* potentials on both sites showed a midday minimum and an afternoon rise. Leaf water potentials of *Geum* on both sites and of *Deschampsia* on site 5 remained near the midday value throughout the afternoon, while those of *Kobresia* and *Deschampsia* on site 3 and *Caltha* on site 5 continued to decline. As the sites dried out, the diurnal pattern seems to have

shifted from midday depression and afternoon recovery, to midday depression and afternoon continuance of the depression, to a continual decrease throughout the day.

Following the late July and August rains, the diurnal pattern of leaf water potentials in *Geum, Bistorta,* and *Deschampsia* near the mobile van was one of midday depression and afternoon recovery (Fig. 4). During the day, leaf water potentials of *Deschampsia* were lower than those of *Geum,* which were lower than those of *Bistorta.* Midday values on August 10–11 near the mobile van were lower than those on July 22 at site 3 and lower than those of August 21–22 near the van. Leaf water potentials rose in the evening of August 21 as a cloud layer settled on the site. The clouds lifted at about 2000 h and a strong dry wind occurred which increased transpiration and decreased leaf water potentials. When the winds subsided about midnight, potentials increased.

Water potentials measured on plant parts of *Geum* and *Deschampsia* showed no differences between old and new leaves (*t*-test, $P > .05$) (Table 1). Potentials in the inflorescence were lower than those in the leaves (*t*-test, $P < .05$) in both species. In *Deschampsia* the leaves were 12–13 bars lower than the inflorescence, and in *Geum* 4–5 bars lower.

The relationships of leaf water potential and RSD of *Bistorta* and *Caltha* close to the van showed different responses (Fig. 5). Leaf water potentials of *Bistorta* decreased at a rate of −0.8 bars/% RSD

TABLE 1. Mean and 95% confidence intervals for leaf water potentials of different plant parts of *Deschampsia* and *Geum*. Sample size is ≥ 10 in all cases. Water potentials were measured on site 3 during sunny conditions between 1000 and 1300 h.

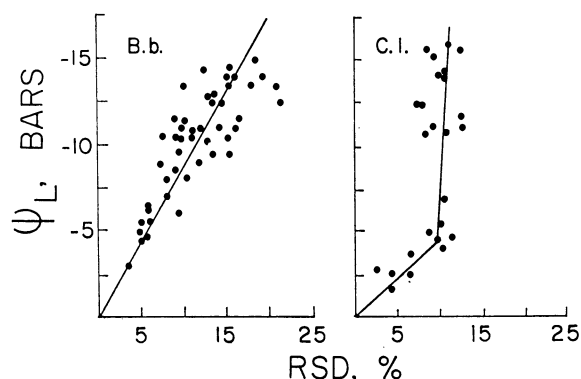| Date	First or second leaf	Newest leaf	Inflorescence
		Deschampsia	
July 10	−23.3 ± 2.5	−18.9 ± 2.0	—
August 7	−17.6 ± 1.1	−19.9 ± 1.9	−8.2 ± 2.0
August 10	−20.5 ± 1.7	−23.1 ± 1.9	−8.7 ± 1.5
		Geum	
July 10	−12.6 ± 3.0	−12.5 ± 1.0	−8.2 ± 0.8
August 10	−17.8 ± 2.2	−17.6 ± 2.2	—

FIG. 5. Relation between leaf water potential (Ψ_L) and relative saturation deficit (RSD) for *Bistorta* (B.b.) and *Caltha* (C.l.).

between 3% and 21% RSD. Leaf water potentials of *Caltha* decreased at a rate of −0.5 bars/% RSD to a RSD of about 10%. Above 10%, leaf water potentials decreased at a rate of about −10 bars/% RSD.

Resistances of Bistorta and Caltha

Both *Bistorta* and *Caltha* had higher leaf resistances on one surface than on the other. *Bistorta* had the highest resistances on the adaxial surface: usually between 20 and 141 $s \cdot cm^{-1}$ with a few values below 20 $s \cdot cm^{-1}$; whereas abaxial leaf resistances were between 0.8 and 13 $s \cdot cm^{-1}$. In contrast, *Caltha*, adaxial leaf resistances were lowest—between 1 and 17 $s \cdot cm^{-1}$; abaxial leaf resistances were between 15 and 35 $s \cdot cm^{-1}$, with values under 15 $s \cdot cm^{-1}$ when air temperatures were above 15°C.

The morning resistances of *Bistorta* and *Caltha* did not change consistently throughout the season (Spearman rank order correlation, $P > .05$), but the daily patterns of leaf resistances did (Table 2). Morning resistances of *Bistorta* on sites 3 and 5 varied between 0.8 and 4.9 $s \cdot cm^{-1}$. In early July,

TABLE 2. Summary of leaf resistance in $s \cdot cm^{-1}$ of *Bistorta* on sites 3 and 5 and *Caltha* on site 5. Values are means of four measurements

Hour of day	7/5	7/7	7/8	7/12	7/19	7/24	8/2	8/9
			Bistorta—Site 3					
0600–0900	3.2	1.6	2.2	0.8	1.6	2.3	1.6	—
0900–1200	1.4	0.2	1.6	3.1	—	5.0	4.9	1.8
1200–1500	1.2	1.1	2.5	1.5	1.1	—	—	1.8
			Bistorta—Site 5					
0600–0900	3.4	2.0	3.1	2.2	4.9	1.6	1.0	—
0900–1200	1.4	0.4	3.1	2.8	—	3.6	3.2	0.8
1200–1500	1.3	3.8	5.9	4.7	4.9	—	—	1.6
			Caltha—Site 5					
0600–0900	2.0	2.4	1.1	2.7	1.6	1.0	2.0	—
0900–1200	2.0	0.2	2.4	1.6	—	4.0	5.3	2.9
1200–1500	2.4	3.0	2.8	2.8	9.6	—	—	5.7

morning resistances were higher on site 5, but in late July and early August they were higher on site 3. Morning resistances of *Caltha* varied between 1.0 and 2.7 $s \cdot cm^{-1}$. The daily patterns shifted from higher in the morning, lower through late morning and lowest in early afternoon; to higher in the morning, lowest in late morning, and higher in early afternoon; to highest in late morning, with low resistances in early morning and early afternoon; to high resistances in late morning and early afternoon. Resistances of *Bistorta* on site 3 increased from morning to midday after July 7. Resistances of *Bistorta* on site 5 increased from morning to midday after July. Leaf resistances of *Caltha* increased from morning to midday through July and early August. The late July rain did not seem to change the daily pattern. Midday resistances were 2–3 $s \cdot cm^{-1}$ higher than morning resistances in late July and early August.

Along the full moisture gradient, the daily pattern changed throughout the season (Fig. 6). On July 5 leaf resistances increased after 0800 h on site 1 but continued low into the afternoon on sites 2, 3, 4, and 5. Minimum resistances of *Bistorta* were usually about 0.8 $s \cdot cm^{-1}$ and of *Caltha* usually about 1.6 $s \cdot cm^{-1}$. However, one measurement of 0.2 $s \cdot cm^{-1}$ was made on each species. On July 12, leaf resistances were increasing on all sites and were higher later in the day than at 0700–0900 h. On July 19, resistances at 1400 h were consistently higher than at 0800 h. On sites 1, 2, and 3, resistances decreased after 0800 h then increased in the early afternoon. On sites 4 and 5 resistances increased in late morning and decreased in the afternoon. On July 19, minimum resistances of *Bistorta* were about 1.0 $s \cdot cm^{-1}$ and of *Caltha* about 4.2 $s \cdot cm^{-1}$.

The relation of leaf resistances to leaf water potentials differed in *Bistorta* and *Caltha* (Fig. 7). In *Bistorta*, resistances increased with water potentials between −1 and −13 bars at a rate of 0.15
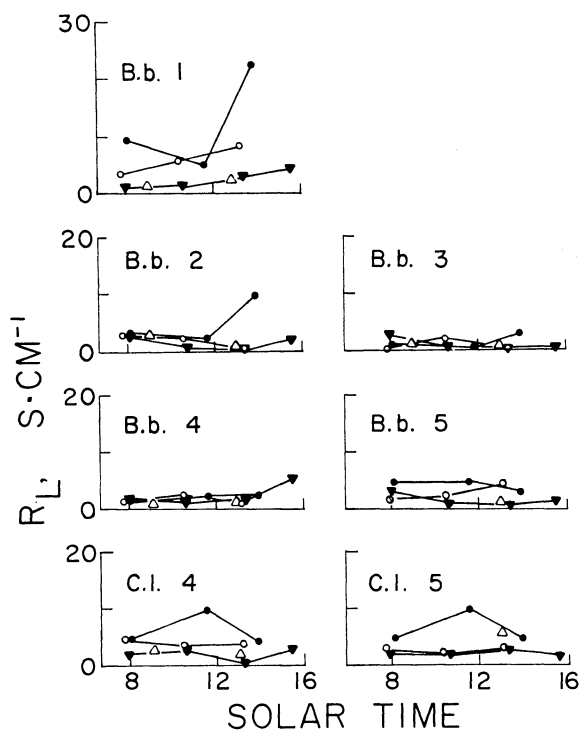
FIG. 6. Daily courses of leaf resistances (R_L) of *Bistorta* (B.b.) and *Caltha* (C.l.) on sites 1–5 on July 5 (▼), 12 (○), and 19 (●) and August 9 (△).

FIG. 7. Relation between leaf resistances to water loss (R_L) and leaf water potential (Ψ_L) in *Bistorta* (B.b.) and *Caltha* (C.l.). (○) denotes measurements on plants near the van; (●) denotes those made on site 5.

$s \cdot cm^{-1} \cdot bar^{-1}$. By extrapolating to 0 bars, minimum resistance would be 0.7 $s \cdot cm^{-1}$. In *Caltha* resistances increased with water potentials between −4 and −13 bars at a rate of about 0.07 $s \cdot cm^{-1} \cdot bar^{-1}$. By extrapolating to 0 bars, the minimum leaf resistance would be 1.8 $s \cdot cm^{-1}$. Below −16 bars resistances of *Caltha* increased sharply with small decreases in water potential. There was no indication of such a sharp break in *Bistorta* at −16 bars. The relationship of leaf resistance to leaf water potential in *Bistorta* probably differed on sites 3 and 5 since the resistances of *Bistorta* differed on these sites while the leaf water potentials were the same.

As leaf temperatures increased, leaf resistances of *Geum*, *Bistorta*, and *Deschampsia* at high light intensities decreased. Resistance of *Geum* decreased at a rate of about 0.3 $s \cdot cm^{-1} \cdot °C^{-1}$ to 20°C and of *Deschampsia*, at about 0.06 $s \cdot cm^{-1} \cdot °C^{-1}$ to 15°C. Resistances of both *Geum* and *Bistorta* were lowest between 20° and 25°C and of *Deschampsia* at 15°C. Resistances increased above these temperatures, perhaps because of leaf water stress induced by the higher vapor density deficits. In studies in which vapor density deficits were not allowed to develop (Stålfelt 1962, Walker and Zelitch 1963, Zelitch 1965), stomatal apertures continued to open as temperatures increased to 30°C.

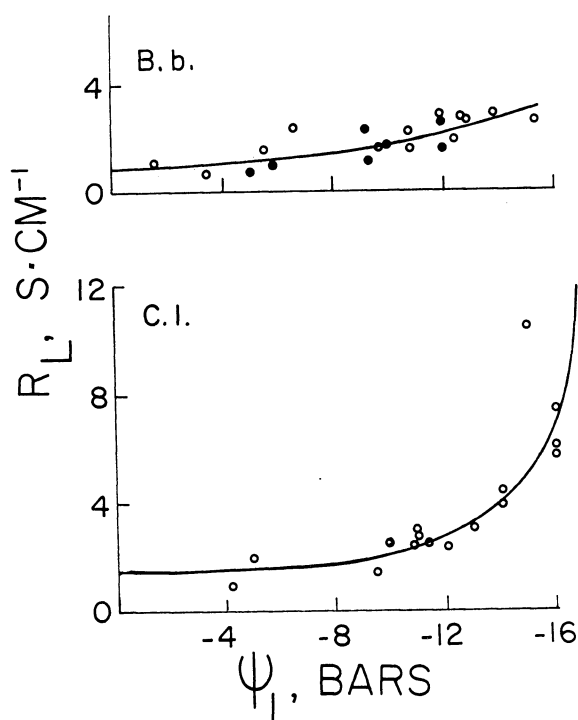A complete response curve for leaf resistance and solar radiation could not be measured since the measurements could be made only at dawn because of high radiation intensities later in the day, and because at dawn condensation in the airlines was common. In the few good measurements obtained, the leaf resistances of all species were minimal at 0.20–0.30 $ly \cdot min^{-1}$.

Root and soil resistances were calculated from midday vapor density deficits, leaf resistances, and leaf and soil water potentials measured on July 2, 9, and 17 and August 10. The mean root and soil resistance, using one midday reading from each of the 4 days, for *Bistorta* were 0.89 × 10⁴ and 0.82 × 10⁴ $s \cdot cm^{-1} \cdot bar^{-1}$ for sites 3 and 5, respectively, and for *Caltha* 0.61 × 10⁴ $s \cdot cm^{-1} \cdot bar^{-1}$.

DISCUSSION

Leaf water potentials measured in this study were lower than previously reported for tundra plants. Rochow (1967) reported that on Niwot Ridge during a dry summer leaf water potentials of *Thalaspi alpestre* were above −10 bars. Kuramoto and Bliss (1970) found that on their meadow site in the Olympic Mountains leaf water potentials of *Caltha leptosepala* were always above −11.4 bars. Billings

and Mooney (1968) reported relatively high potentials on Niwot Ridge. Hillier (1970) observed that net photosynthetic rates of *Deschampsia caespitosa* decreased abruptly with leaf water potentials below −10 bars. However, we found minimum potentials of all species below −15 bars and potentials of −40 bars in *Kobresia*. Leaf water potentials of monocotyledonous and dicotyledonous species differed. In *Kobresia* and *Deschampsia* they were always lower than in *Geum, Bistorta,* and *Caltha*; this may be due to differences either in their rooting depths, root to shoot ratios, or transpiration rates. *Kobresia* and *Deschampsia* have fibrous root systems; *Geum, Bistorta,* and *Caltha* have tap roots or rhizomes.

Measurements of leaf resistances and estimates of transpiration rates for alpine tundra species are rare. Leaf resistances reported in this study are higher than published estimates for most agricultural species, but lower than those for naturally occurring species (Miller and Gates 1967, Kanemasu and Tanner 1969, Millar et al. 1971, Elfing et al. 1972, Small 1972). Mooney et al. (1965) reported transpiration rates for *Polygonum bistortoides* (*Bistorta bistortoides*) and *Caltha howellii*. Leaf resistances calculated from their maximum observed transpiration rates were 1.2 and 3.6 s·cm⁻¹, respectively. The calculated resistance of *Bistorta* is similar to the minimum resistances of *Bistorta* reported in this study, but the resistance of *C. howellii* is higher than the minimum resistance for *C. leptosepela*. Moore et al. (1973) reported leaf resistances of 27.1, 4.9, 1.8, and 6.5 s·cm⁻¹ for *Kobresia, Geum, Bistorta,* and *Deschampsia*, measured at 25°C in midsummer. The high leaf resistances of *Kobresia* suggest that it is not active in midsummer. This agrees with the hypothesis that *Kobresia* is most active in spring and early summer (Bliss 1971) and with the low leaf water potentials of *Kobresia* reported in this study.

Leaf resistances of *Caltha* on the wet site tended to increase sooner and more rapidly throughout the day than those of *Bistorta* on the dry site. This is similar to the pattern found in other studies. Mooney et al. (1965) found transpiration decreasing earlier in *Caltha* than in *Ivesia gordonii*, a dry-site species, as soil moisture decreased. Klikoff (1965) found that net photosynthetic rates decreased abruptly when leaf water potentials decreased below −5 bars in *Calamagrostis breweri*, a moist-site species, and below −15 bars in *Carex exserta*, a dry-site species. The decrease in net photosynthetic rates may be due to stomatal closure, since Troughton (1969) and Boyer (1970) found little effect of leaf water potential on photosynthesis in the ranges of water potentials usually found in their plants.

The explanation of the different daily courses of

leaf resistances throughout the season also appears to lie in the relationship between leaf resistance and leaf water potential. Such relationships have not been emphasized in previous studies. Leaf resistance–leaf water potential curves have been reported only for agricultural species such as snap beans (Kanemasu and Tanner 1969) and onions (Millar et al. 1971). As soil moisture and soil water potential decrease, leaf water potential also decreases but at a faster rate than soil water potentials in order to maintain a sufficient gradient in water potential for water uptake. In *Caltha* and *Bistorta*, on the wet site, this decreasing leaf water potential is soon accompanied by greater leaf resistances, decreasing leaf water loss. In *Bistorta*, on the dry site, and perhaps in *Ivesia* also, leaf resistances increase less with decreasing leaf water potential. This is consistent with the earlier concepts of critical water contents for stomatal closure of mesic and xeric species and for the differences within a species on different microhabitats (Stålfelt 1929, 1955, Hygen 1951, 1953, Jarvis and Jarvis 1963, Bannister 1964, 1971, Anderson and McNaughton 1973). Since photosynthesis is usually reduced by increased leaf resistances, the photosynthetic rates of the dry-site plants are affected less by decreases in leaf water potentials as the soil dries out than are wet-site plants.

As the season progressed, several patterns seemed to emerge in the diurnal courses of leaf resistance and leaf water potential, which were apparently related to water stress. First, leaf resistance patterns changed from one of stomatal opening in the morning and continual low resistances throughout the day, to stomatal opening in the morning and a gradual increase in leaf resistance from midday, and finally to stomatal opening in the morning, high resistances through midday with some afternoon recovery. Similarly, three daily patterns of leaf water potential were seen throughout the season. At the beginning of the season leaf water potentials decreased to a midday low, followed by an afternoon recovery. As water stress appeared, leaf water potentials decreased to a midday value and remained at this value through the afternoon; as water stress increased, leaf water potentials decreased continually throughout the day.

Jarvis and Jarvis (1963) stressed the importance of knowing the interrelationships between leaf resistance, water potential, and water content, in order to understand the water relations of a species. The results of this study support their contention. Interpretation of the diurnal courses of leaf resistance and water potential throughout the season is difficult without an understanding of how leaf resistance is affected by water potential and how water potential is affected by the RSD, the root and soil resistances, and the transpiration rate.

The role of water in limiting the distribution of the five species studied is indicated in the daily courses of leaf water potentials and leaf resistance. The daily courses of water potential from sites 3 and 5 early in the season indicate that all species except *Kobresia* are equally adapted to the sites on which they are found since all show an afternoon recovery. The absence of this recovery in *Kobresia* may be due to its relative inactivity. However, later in the season at the peak of drought stress, those species occurring on more xeric sites (*Geum* and *Bistorta* on site 5, *Bistorta* on site 3) showed a leaf water potential pattern with an afternoon recovery; and species at the xeric end of their distribution (*Caltha* on site 5, *Deschampsia* on site 3) showed a continual decrease in leaf water potentials throughout the day. Again the pattern for *Kobresia* can be explained if the species is not active in midsummer. It is expected that leaf water potentials of a species at the xeric end of its distribution will frequently be in the portion of the leaf resistance–leaf water potential curve where resistances increase rapidly in response to changes in potential, and that the increased leaf resistances will also restrict production. This study indicated that water stress can be high in the alpine tundra and may limit primary production, and that, in order to study the effects of plant water relations on plant distribution, the total soil–plant–atmosphere system should be characterized. This has not been done in most physiological ecology research.

LITERATURE CITED

Anderson, J. E. 1971. Effects of water stress induced by low soil temperatures on altitudinally diverse plant populations. Ph.D. Thesis. Syracuse Univ., Syracuse, N.Y.

Anderson, J. E., and S. J. McNaughton. 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. Ecology 54:1220–1233.

Bannister, P. 1964. Stomatal responses of heath plants to water deficits. J. Ecol. 52:151–158.

———. 1971. The water relations of heath plants from open and shaded habitats. J. Ecol. 59:51–64.

Barry, R. G. 1973. A climatological transect of the east slope of the Front Range, Colorado. Arct. Alp. Res. 5:89–110.

Billings, W. D., and L. C. Bliss. 1959. An alpine snowbank environment and its effect on vegetation, plant development, and productivity. Ecology 40:388–397.

Billings, W. D., and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biol. Rev. 43:481–529.

Bliss, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. Ecol. Monogr. 26:303–337.

———. 1971. Arctic and alpine plant life cycles. Annu. Rev. Ecol. Syst. 2:405–438.

Boyer, J. S. 1970. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 46:236–239.

Cox, C. F. 1933. Alpine plant succession on James Peak, Colorado. Ecol. Monogr. 3:300–372.

Elfing, D. C., M. R. Kaufmann, and A. E. Hall. 1972. Interpreting leaf water potential measurements with a model of the soil–plant–atmosphere continuum. Physiol. Plant. 27:161–168.

Hillier, R. D. 1970. The influence of water on growth and development of alpine plants in the Medicine Bow Range, Wyoming. Ph.D. Thesis. Duke Univ., Durham, N.C.

Honert, T. H. van den. 1948. Water transport in plants as a catenary process. Discuss. Faraday Soc. 3:146.

Hygen, G. 1951. Studies in plant transpiration. I. Physiol. Plant. 4:57–183.

———. 1953. Studies in plant transpiration. II. Physiol. Plant. 6:106–133.

Jarvis, P. G., and M. S. Jarvis. The water relations of tree seedlings. IV. Some aspects of the tissue water relations and drought resistance. Physiol. Plant. 16:501–516.

Kanemasu, E. T., and C. B. Tanner. 1969. Stomatal diffusion resistance of snap beans. I. Influence of leaf water potential. Plant Physiol. 44:1547–1552.

Kanemasu, E. T., G. W. Thurtell, and C. B. Tanner. 1969. Design, calibration, and field use of a stomatal diffusion porometer. Plant Physiol. 44:881–885.

Klikoff, L. 1965. Photosynthetic response to temperature and moisture stress of three timberline meadow species. Ecology 46:516–517.

Koch, W., O. L. Lange, and E. Schulze. 1971. Ecophysiological investigations on wild and cultivated plants in the Negev Desert. I. Methods: A mobile laboratory for measuring carbon dioxide and water vapour exchange. Oecologia 8:296–309.

Kuramota, R. T., and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecol. Monogr. 40:317–347.

Marr, J. W. 1967. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies. Series in Biology, no. 8, Univ. Colorado Press, Boulder. 134 p.

Marr, J. W., J. M. Clark, W. S. Osburn, and M. W. Paddock. 1968. Data on mountain environments. III. Front Range, Colorado, four climax regions, 1959–1964. University of Colorado Studies. Series in Biology, no. 8. Univ. Colorado Press, Boulder. 181 p.

Millar, A. A., W. R. Gardner, and S. M. Goltz. 1971. Internal water status and water transport in seed onion plants. Agron. J. 63:779–784.

Miller, P. C., and D. M. Gates. 1967. Transpiration resistance in plants. Am. Midl. Nat. 77:77–85.

Mooney, H. A., R. D. Hillier, and W. D. Billings. 1965. Transpiration rates of alpine plants in the Sierra Nevada of California. Am. Midl. Nat. 74:374–386.

Moore, R. T., J. Ehleringer, P. C. Miller, M. Caldwell, and L. Tieszen. 1973. Gas exchange studies of four

alpine tundra species at Niwot Ridge, Colorado. *In* L. C. Bliss and F. E. Wielgolaski [ed.], Primary production and production process, Tundra Biome. Univ. Alberta Printing Service, Edmonton.

Morrow, P. A., and R. O. Slatyer. 1971. Leaf resistance measurements with diffusion porometers: Precautions in calibration and use. Agric. Meteorol. **8**:223–233.

Osburn, W. S. 1958. Ecology of winter snow-free areas of the alpine tundra of Niwot Ridge, Boulder County, Colorado. Ph.D. Thesis. Univ. Colorado, Boulder.

Rawlins, S. L. 1963. Resistance to water flow in the transpiration stream, p. 69–84. *In* I. Zelitch [ed.], Stomata and water relations in plants. Conn. Agric. Exp. Sta. Bull. 664, New Haven.

Rochow, J. L. 1967. The ecology of *Thalaspi alpestre* in the Central Rocky Mountains along altitudinal gradients. Ph.D. Thesis. Duke Univ., Durham, N.C.

Salisbury, E. B., and G. G. Spomer. 1964. Leaf temperatures of alpine plants in the field. Planta **60**:497–505.

Scott, D., and W. D. Billings. 1964. Effects of environmental factors on standing crop and productivity of an alpine tundra. Ecol. Monogr. **34**:243–270.

Small, E. 1972. Water relations of plants in raised sphagnum peat bogs. Ecology **53**:726–728.

Stålfelt, M. G. 1929. Die Abhangigkeit der Spaltoffnungsreaktionen von der Wasserbilanz. Planta **8**:287–340.

———. 1955. The stomata as a hydrophotic regulator of the water deficit of the plant. Physiol. Plant. **8**:572–593.

———. 1962. The effects of temperature on opening of the stomatal cells. Physiol. Plant. **15**:772–779.

Tranquillini, W. 1963. Climate and water relations of plants in the sub-alpine region, p. 153–167. *In* A. J. Rutter [ed.], The water relations of plants, Dorking, England. Blackwell Scientific Publications, Oxford.

———. 1964. The physiology of plants at high altitude. Annu. Rev. Plant Physiol. **15**:345–362.

Troughton, J. H. 1969. Plant water status and carbon dioxide exchange of cotton leaves. Austr. J. Biol. Sci. **22**:289–302.

Walker, D. A., and I. Zelitch. 1963. Some effects of metabolic inhibitors, temperature, and anaerobic conditions on stomatal movement. Plant Physiol. **38**:390–396.

Weber, W. A. 1967. Rocky mountain flora. Univ. Colorado Press, Boulder. 437 p.

Zelitch, I. 1965. Environmental and biochemical control of stomatal movement in leaves. Biol. Rev. **40**:463–482.