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14. Some Aspects of Water Relations of Arctic and Alpine Regions

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Introduction

The objectives of this study were to measure certain aspects of the water relations of selected plants occurring in the arctic tundra and alpine tundra and to assess the possible role of water limitation on primary production in these two ecosystems. At low leaf water potentials, water limitation of production may occur by stomatal closure restricting water loss and photosynthesis or by reduced growth because of decreased cell turgor. Jarvis and Jarvis (1963) stressed the importance of knowing the interrelationships between leaf resistance, water potential, and water content, before the water relations of a species could be understood. Hence, to study the effects of plant water relations on plant distribution and production the total soil-plant-atmosphere system should be characterized.

In the arctic there have been few studies on plant water relations. Billings and Mooney (1968) concluded that at Barrow, Alaska, plant water stress was minor with leaf water potentials above -4 to -5 bars. However, Courtin and Mayo (1975) report lower leaf water potentials (-25 to -60 bars) at Devon Island, Canada, and state that, with the exception of data from Barrow, arctic plants generally appear to have low leaf water potentials even when growing in water.

In the alpine Cox (1933) suggested that production may be limited by length of growing season, low temperatures, and moisture. Scott and Billings (1964) and Hillier (1970) considered soil moisture as a principal factor limiting plant growth in the alpine. 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. Kuramoto and Bliss (1970) reported that, in the subalpine communities of the Olympic Mountains in Washington, net photosynthesis of several species decreased as soil water potential decreased. 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, while transpiration of plants from dry sites remained constant throughout the day. Discussion of the arctic and alpine data presented here may be found in Stoner and Miller (1975) and Ehleringer and Miller (1975).

Conceptual Framework

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 forces for water absorption across root and soil resistances. Water loss from the leaf 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 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 and is portrayed graphically in Figure 1.

The curvilinear relationship between transpiration and leaf resistance is given in the upper right quadrant. As leaf temperatures increase, transpiration will increase at any given leaf resistance. Transpiration rates at higher leaf temperatures and the same ambient water vapor density are shown by the dashed lines.

The relationship between leaf resistance and relative saturation deficit (RSD), a measure of the water lost from a leaf relative to the turgid state, is shown in the lower right quadrant. At full turgidity (an RSD of zero) leaf resistances are at

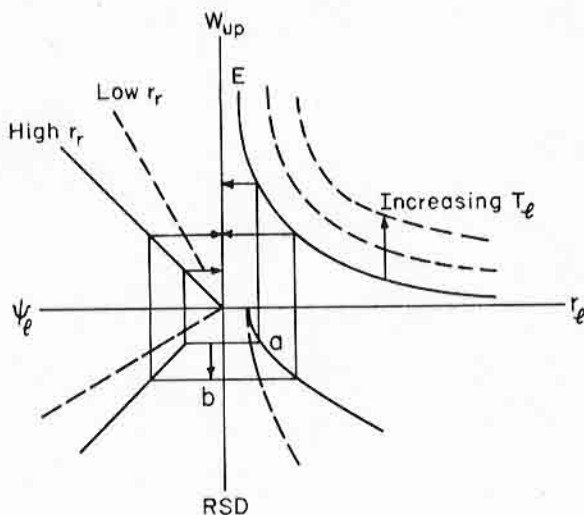


Figure 1. Diagram illustrating the interrelations between transpiration (E), leaf resistance (r_l), relative saturation deficit (RSD), leaf water potential (Ψ_l), water uptake (W_{up}), and root resistance (r_r).

minimum values, assuming light intensities are not low enough to inhibit stomatal opening. As the RSD increases the leaf resistance increases, and the sensitivity of leaf resistance to changes in RSD will differ by species. The typical pattern is that species from wet habitats (solid line) have a sharp increase in leaf resistance as RSD increases, and species from drier habitats (dashed line) have a much lower sensitivity of leaf resistance to RSD. The relationship between leaf water potential and RSD is shown in the lower left quadrant. Species with a leaf water potential more sensitive to changes in RSD are shown by a dashed line.

The relationship of water uptake to leaf water potential, assuming a substrate water potential of zero, is shown in the upper left quadrant. Root resistance is the resistance of the entire absorbing root mass which is related to the total surface area. Since species differ in their total root biomass and their total root surface area to total root biomass ratios (i.e., fibrous versus tap root), their root resistances will also differ.

A daily course of plant water relations can be followed with these graphs. For example, starting at point "a" on the leaf resistance-RSD curve, the transpiration rate implied by that leaf resistance is given by the arrow up to the transpiration-leaf resistance curve and across to the transpiration axis. The rate of water uptake can be obtained by following from point "a" horizontally across to the water potential-RSD curve, up to the water potential-root resistance curve and across to the water uptake axis. A plant with the leaf resistance implied by the "a" arrow will have a rate of transpiration exceeding the rate of water uptake. This means that the water content of the leaf will decrease and RSD will increase. The increase in RSD is shown by the "b" arrows. At this higher RSD a higher leaf resistance occurs which produces a lower transpiration rate. The new RSD also implies a lower leaf water potential and greater water uptake. In this case transpiration and water uptake are equal, hence, the RSD will be maintained at this level. The effect of increasing leaf temperatures on the system can be explored with this diagram as can the effect of different relationships among leaf resistance, water potential, RSD, and root system resistance.

Methods

The arctic study was conducted near Barrow, Alaska, at sites 2 and 4 during the summer of 1972 and at site 1 during the summer of 1973. Leaf water potentials and the relationship between leaf water potential and relative saturation deficit were measured in *Arctophila fulva*, *Dupontia fisheri*, *Carex aquatilis*, *Eriophorum angustifolium*, *Potentilla hyparctica*, and *Salix pulchra*. *In situ* leaf resistances to water loss and root resistances to water absorption were measured only in *Dupontia*, *Carex*, and *Eriophorum*.

The alpine study was conducted on Niwot Ridge in the Front Range in central Colorado (40°02' N, 105°33' W) during the summer of 1972. The study sites were located at the 3500-m elevation in the area called the Saddle. Five sites were chosen along a moisture gradient, site 1 being the driest and site 5 the wettest.

Site 1 was on the east knoll of the Saddle in fellfield tundra where the vegetation consisted predominantly of *Silene acaulis* and *Kobresia myosuroides*. Site 2 was in an area dominated by *Kobresia*. Site 3 was exposed to wind and kept snow free throughout the winter and contained a diversity of species including *Geum rossii*, *Bistorta bistortoides*, and *Deschampsia caespitosa*. Site 4 occurred in the center of a trough and was dominated by *Salix nivalis*. Site 5 was protected from prevailing winds, covered by snow during the winter, and received meltwater from snow until the end of June. Vegetation consisted primarily of *Geum*, *Bistorta*, *Deschampsia*, *Caltha leptosepala*, and *Artemesia scopulorum*. The species studied were *Kobresia*, *Geum*, *Bistorta*, *Deschampsia*, and *Caltha*. *Kobresia* occurred only on sites 1, 2, and 3. *Geum* and *Bistorta* occurred on all sites. *Deschampsia* occurred on sites 3, 4, and 5. Leaf water potentials were measured in all species; while *in situ* leaf resistances to water loss, the relationship between leaf resistance and leaf water potential, and the relationship between leaf water potential and relative saturation deficit were measured only in *Bistorta* and *Caltha*.

A scholander-type pressure chamber was used to measure leaf water potentials. At Barrow leaf water potentials were measured every 2 to 3 hr in 1972 on 30 June to 2 July, 6 to 8 July, 23 to 26 July, 2 to 4 August, and 16 to 17 August; while in 1973 water potentials were measured at 3-hr intervals during two 24-hr periods, 29 to 30 July and 3 to 4 August. At Niwot, leaf water potentials were measured every 2 weeks between 15 June and 22 August, and every 3 hr throughout the day on sites 3 and 5, on 30 June, 22 July, 10 to 11 August, and 21 to 22 August.

Relative saturation deficit (RSD) (Barrs, 1968) was measured at Niwot by excising leaves and taking 0.635-cm diameter punches from a leaf. At Barrow leaves were excised and cut into 1-cm long pieces. Usually less than 2 min elapsed between leaf excision and the fresh weight measurement. Leaves were floated on distilled water at room temperature until turgid and reweighed to determine the turgid weight. RSD was calculated as the difference between the turgid and fresh weight divided by the turgid weight and expressed as a percentage.

The relationship between leaf water potential and RSD was determined at Barrow by measuring leaf water potentials while four to six adjacent leaves were taken for RSD measurements. The means of six water potentials and three RSD measurements were used for each point. At Niwot, the water potential of one leaf of a pair was measured while the other leaf was taken to measure the RSD.

At Niwot *in situ* leaf resistance to water loss was measured with a porometer (Kanemasu et al., 1969). Due to the size of the aperture on the porometer, only the broader leaves of *Bistorta* and *Caltha* could be measured. The porometer and the leaf were shaded to equalize temperatures between the porometer sensor and the leaf surface. The porometer was calibrated at 3500 m at several temperatures covering the range experienced in the field (5 to 20°) to correct for the temperature effects on the sensor (Morrow and Slatyer, 1971). Resistance of the upper and lower leaf surfaces were measured and the total leaf resistance was calculated as the mean of the parallel resistances for both surfaces. At Barrow *in*

situ leaf resistances were measured with a single leaf cuvette, through which dried air was drawn.

The relationship between leaf resistance and leaf water potential was determined for *Bistorta* and *Caltha* at Niwot by measuring resistances and water potentials on groups of five leaves selected randomly from 1 m² quadrats. Measurements were taken only under high light intensities.

In order to determine the relationship between leaf resistance and RSD at Barrow, the method of measuring transpiration rates by repeatedly weighing cut leaves was modified (Hygen, 1951; Bannister, 1971; Waggoner and Turner, 1971). Groups of cut leaves were weighed every 2 min for 40 min on a Mettler balance (0.1 mg accuracy) while monitoring ambient and dew point temperatures inside the weighing chamber. Assuming that the leaves were at ambient temperature, leaf resistances were calculated from:

$$r_l + r_a = (VS_1 - V_a)(W_t - W_{t+1})^{-1} A(\Delta t)$$

where $r_l + r_a$ = the combined leaf and air resistance,

VS_1 = the saturation water vapor density at leaf temperature,

V_a = the ambient vapor density,

W_t = the weight at time t ,

A = the area of leaves in the chamber, and

Δt = the time between weight measurements.

The RSD of the leaves was calculated by using the weight at each time interval as the fresh weight. The initial RSD and turgid weight were measured on other leaves collected from the same field area during the same period.

Cuticular resistances were determined for the Barrow species from the final linear section of the drying curve. Hygen (1951) designated three phases in the drying curve: a rapid linear decrease in weight (stomatal phase); a curvilinear phase, characterized by a slowing of the rate of change in weight (closing phase); and a linear decrease (cuticular phase). The slope of this final phase is the cuticular transpiration.

Root resistances were calculated using leaf resistance and leaf water potential values that were measured simultaneously on adjacent plants. By assuming that at the time of measurement transpiration and water uptake are equal:

$$r_r + r_s = (\Psi_s - \Psi_l)(r_a + r_l)(VS_1 - V_a)^{-1}$$

where Ψ_s is the soil water potential and Ψ_l is the leaf water potential. The calculated root resistance is the resistance of the entire root mass plus the soil resistance to water flow. Most measurements were made during the mid-morning to ensure that the plants were not recovering from any water stress and hence violating the assumed equality between loss and uptake.

At Barrow, root resistances were also measured in an area where soil temperatures were raised above ambient by pipes carrying heated water which were buried 3 yr earlier.

Results

Barrow

The relationship between leaf water potential and RSD was linear throughout the range of RSD measured in the field (Figure 2). Slopes in bars RSD⁻¹ were -1.82 for *Arctophila*, -1.06 for *Dupontia*, -1.05 for *Carex*, -0.57 for *Eriophorum*, -0.73 for *Potentilla*, and -0.95 for *Salix*. The responses of leaf resistance to

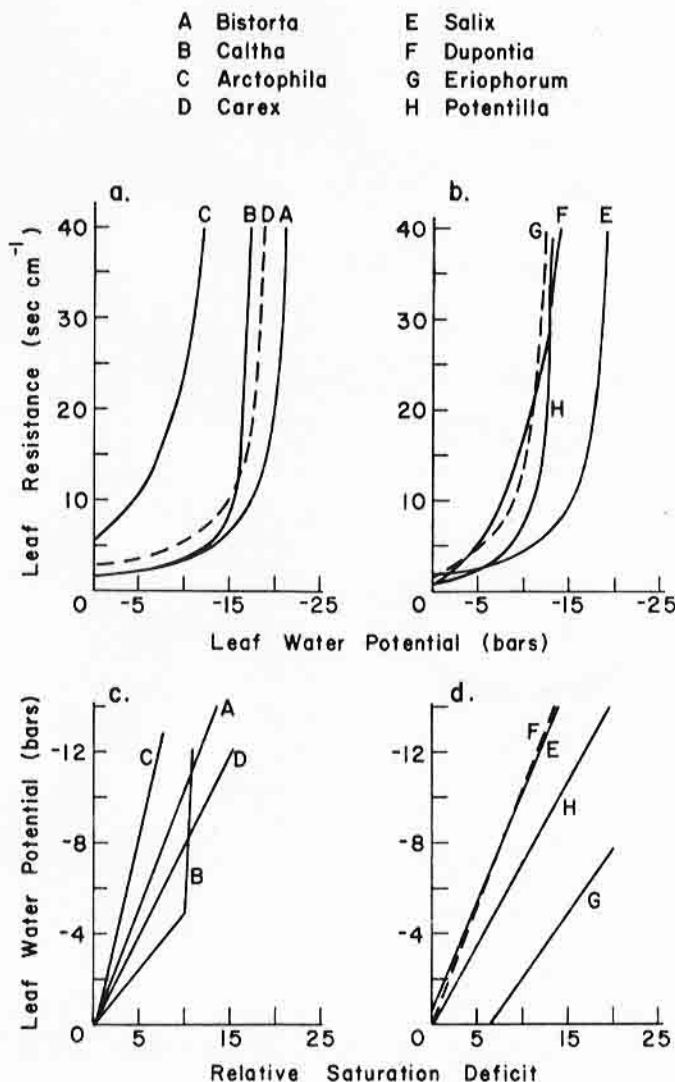


Figure 2. Relationships between relative saturation deficit (RSD) and leaf water potential for the arctic and alpine species and between leaf water potential and leaf resistance to water loss. Data from Stoner and Miller (1975) and Ehleringer and Miller (1975).

Table 1. Cuticular Resistances, Turgid Leaf Densities, and the 95% Confidence Limits for Turgid Leaf Densities for the Six Barrow Species and Some Other Plants^a

Species	Cuticular resistance (sec cm ⁻¹)	Turgid density (mg cm ⁻²)
<i>Arctophila</i>	38.7	24.5 ± 2.3
<i>Dupontia</i>	29.4	19.0 ± 2.6
<i>Carex</i>	22.4	17.0 ± 1.2
<i>Eriophorum</i>	11.8	22.1 ± 0.9
<i>Potentilla</i>	37.0	19.8 ± 3.1
<i>Salix</i>	15.6	22.1 ± 1.0
Shade plants ^b	20.0	
Xerophytes ^b	>200.0	
Tomato ^c	20.0	
Bean ^c	20.0	
Cotton ^d	64.4	

^a Unless noted, data are from this study.

^b Slatyer (1967).

^c Kuiper (1961).

^d Slatyer and Bierhuizen (1964).

changes in RSD showed no signs of reaching a plateau, but continued to increase with increasing RSD, similar to other studies (Kanemasu and Tanner, 1969; Troughton, 1969; Millar et al. 1971).

By combining the relationships between leaf resistance and RSD and leaf water potential, relationship between leaf resistance and leaf water potential is obtained (Fig. 2). The leaf resistances of *Arctophila* and *Dupontia* increased immediately as leaf water potential dropped below 0 bars. Resistances of the other species increased more slowly at first, then rapidly below a water potential which varied with each species. Leaf water potentials at which leaf resistances of 20 sec cm⁻¹ occurred were -9.0 for *Arctophila*, -11.0 for *Dupontia*, -17.5 for *Carex*, -11.0 for *Eriophorum*, -13.0 for *Potentilla*, and -18.0 for *Salix*.

Minimum leaf resistances, obtained by extrapolating to zero water potential, were 6.0 sec cm⁻¹ for *Arctophila*, 1.0 sec cm⁻¹ for *Dupontia*, 3.0 sec cm⁻¹ for *Carex*, 2.0 sec cm⁻¹ for *Eriophorum*, 1.5 sec cm⁻¹ for *Potentilla*, and 2.0 sec cm⁻¹ for *Salix*. Cuticular resistances were between 12 and 39 sec cm⁻¹. Turgid leaf weights were between 17 and 25 mg cm⁻² (Table 1).

The changes of leaf resistance with either RSD or leaf water potential can be compared among species with the "A" and "B" values of each curve. The "A" value is the RSD or water potential at three times the minimum leaf resistance (leaf resistance at 0 RSD or 0 water potential). The "B" value is the RSD or water potential where maximum leaf resistances occur. A leaf water potential less than the "A" value indicates some stomatal closure; while a water potential lower than "B" indicates complete stomatal closure. "A" and "B" water potential values (bars) were, respectively, -8.2 and -12.0 for *Arctophila*, -2.5 and -14.0 for *Dupontia*, -14.0 and -18.0 for *Carex*, -6.5 and -12.3 for *Eriophorum*, -7.9 and -13.7 for *Potentilla*, and -12.3 and -20.0 for *Salix*.

In situ leaf resistances (Table 2) of *Dupontia* on 12 and 13 July were higher in

the polygon trough than on the ridge (Mann-Whitney U test, $P < 0.05$). Resistances of *Carex* and *Eriophorum* though not significantly different between the trough and ridge, tended to be lower in the trough. Resistances of all species combined were not significantly different between the trough and the ridge (Kruskal-Wallis, $P < 0.05$). Resistances in the afternoon were higher than in the morning or at noon for all species. Resistances of *Carex* and *Eriophorum* remained similar between morning and noon readings but increased in the afternoon; those of *Dupontia* increased throughout the day. Cuvette leaf resistances were lower than the estimates of minimum leaf resistances, probably because of the higher air resistance present in the weighing chamber.

Root resistances were independent of soil temperature but were related to transpiration rates. Within a species, root resistances were not significantly different on the heated and ambient sites (U test, $P > 0.05$). However, root resistances among species on both sites were significantly different (Kruskal-Wallis, $P > 0.05$). Average root resistances (in units of $10^6 \text{ sec cm}^{-1} \text{ bar}^{-1}$) were 10.6 for *Dupontia*, 8.4 for *Carex*, and 5.8 for *Eriophorum*. Minimum root resistances were 1.7 for *Dupontia*, 1.2 for *Carex*, and 0.6 for *Eriophorum*. These resistances occurred at transpiration rates of 198, 222, and 240 $\text{mg of H}_2\text{O cm}^{-2} \text{ min}^{-1}$, respectively.

During the growing season of 1972, midday leaf water potentials indicated that water stress increased; while in 1973, water stress did not increase as the season progressed (Figure 3). Midday leaf water potentials were lower on sunny days, which occurred frequently before mid-July in 1972 and at various times during the season in 1973, than on cloudy days. However, the degree of water stress among species differed. A leaf water potential lower than the water potential at which the leaf resistance is three times the minimum ("A" value) was taken as an indication of water stress. In 1972 *Dupontia* was partially stressed throughout the season, with complete stomatal closure indicated in mid-season. *Carex* showed partial stress at least once during the season. In 1973 *Dupontia* was usually partially stressed, *Arctophila* and *Potentilla* were stressed at times; *Carex*, *Eriophorum*, and *Salix* were under little or no stress. Complete stomatal closure occurred during the growing season in *Arctophila* and *Potentilla*.

Table 2. Summary of Leaf Resistances to water loss in sec cm^{-1} , in Polygon Troughs and Ridges, at Different Times of the Day on 12 and 13 June^a

Species	Solar time		
	1000-1130	1300-1500	1530-1730
	Polygon ridge		
<i>Dupontia</i>	(6) 0.46	(6) 0.77	(6) 0.78
<i>Carex</i>	(6) 0.63	(6) 0.50	(3) 1.20
<i>Eriophorum</i>	(6) 0.77	(6) 0.83	(6) 1.87
	Polygon trough		
<i>Dupontia</i>	(7) 0.83	(6) 1.03	(6) 1.55
<i>Carex</i>	(6) 0.55	(6) 0.63	(6) 0.75
<i>Eriophorum</i>	(6) 0.58	(6) 0.85	(6) 0.78

^a The number of measurements is given in parentheses. All species in each site were measured on each day.

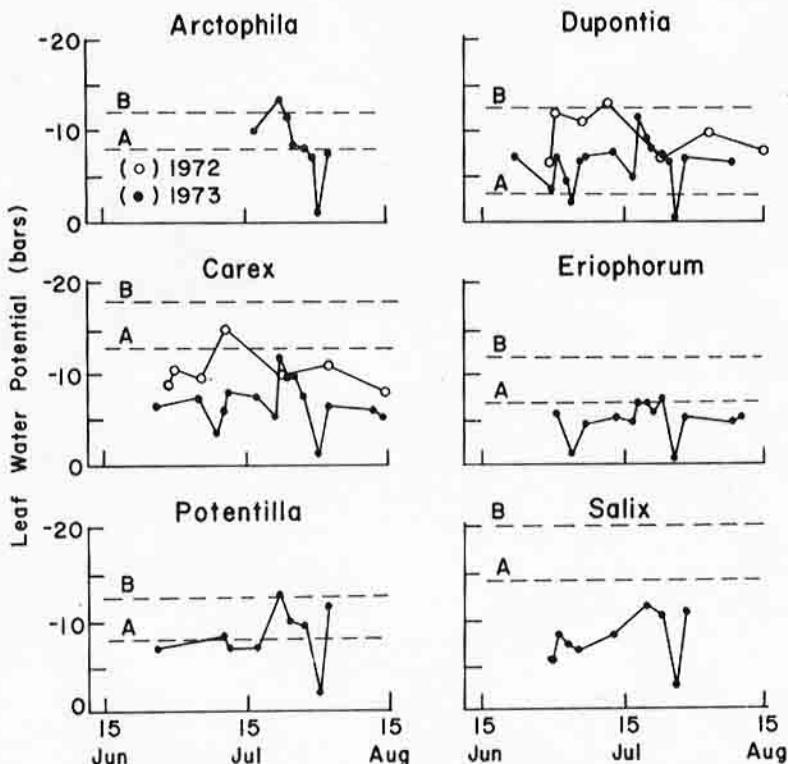


Figure 3. Seasonal course of midday leaf water potentials of the six Barrow species. Adapted from Stoner and Miller (1975) with the permission of the Institute of Arctic and Alpine Research.

Niwot

The relationships of leaf water potential and RSD of *Bistorta* and *Caltha* showed different responses (Fig. 1). *Bistorta* showed a linear response with a slope of -0.8 bars RSD^{-1} , while *Caltha* had a slope of -0.5 below 10% RSD and a slope of -10.0 above 10% RSD.

The relationship of leaf resistances to leaf water potentials differed in *Bistorta* and *Caltha*. The "A" and "B" water potentials were -14 and -22 bars for *Bistorta* and -14 and -17 bars for *Caltha*. Leaf water potentials at which leaf resistances of 20 sec cm^{-1} occurred were -20.0 and -16.0 bars for *Bistorta* and *Caltha*. By extrapolating to 0 bars, the minimum leaf resistance was 0.7 sec cm^{-1} for *Bistorta* and 1.8 sec cm^{-1} for *Caltha*. Turgid leaf weights were 30.0 and 27.0 mg cm^{-2} for *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 abaxial surface. Adaxial leaf resistances were usually between 20 and 141 sec cm^{-1} for *Bistorta* and between 1 and 17 sec cm^{-1} for *Caltha*. Abaxial leaf resistances were between 0.8 and 13 sec cm^{-1} for *Bistorta* and between 15 and 35 sec cm^{-1} for *Caltha*.

The morning leaf resistances of *Bistorta* and *Caltha* did not change consistently through the season (Spearman rank order correlations, $P > 0.05$). Morning leaf resistances were between 0.8 and 4.9 sec cm^{-1} for *Bistorta* and between 1.0 and 2.7 sec cm^{-1} for *Caltha*. Although the morning values of leaf resistance did not change consistently, the daily pattern through the season did change (Figure 4). On 5 July leaf resistances of *Bistorta* decreased after 0800 hr on site 1, while *Bistorta* and *Caltha* on the other sites had low resistances into the afternoon. On 12 July leaf resistances were higher than on 5 July and tended to increase through the day. On 19 July *Bistorta* on sites 1, 2, and 3 had leaf resistances which decreased in late morning and increased in early afternoon. On the same data *Caltha* on sites 4 and 5 had leaf resistances which increased at midday and decreased in the early afternoon.

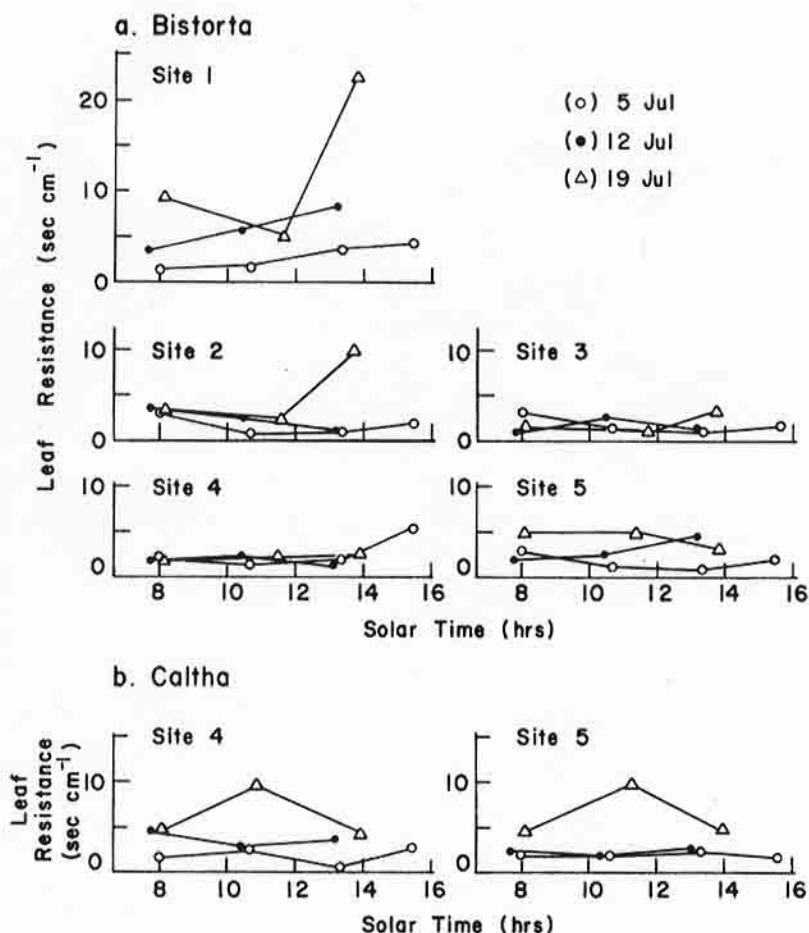


Figure 4. Daily course of leaf resistances of *Bistorta* and *Caltha* on sites 1 through 5 on 5 July (○), 12 July (●), and 19 July (Δ). Adapted from Ehleringer and Miller (1975); Copyright 1975 of the Ecological Society of America.

Table 3. Summary of Maximum and Minimum Dawn Water Potentials Measured through the 1972 Season on Niwot Ridge and Date of Occurrence on Sites 3 and 5

Species	Site 3		Site 5	
	Max Ψ_l	Min Ψ_l	Max Ψ_l	Min Ψ_l
<i>Kobresia</i>	-7 7/7	-22 8/11		
<i>Geum</i>	-3.5 6/30	-10 8/22	-1 6/20	-6.5 8/1
<i>Deschampsia</i>	-5 7/7	-14 8/22	-3 6/20	-7 8/1
<i>Bistorta</i>	-0.5 6/20	-7 8/11	-1 6/20	-5 8/1
<i>Caltha</i>			-2 7/6	-4 8/1

Root and soil resistances were measured on 2, 9, and 17 July, and on 10 August. The mean root-soil resistances were 0.89×10^6 and 0.82×10^6 sec cm⁻¹ bar for *Bistorta* on sites 3 and 5, respectively, and 0.61×10^6 sec cm⁻¹ bar for *Caltha*.

Minimum dawn water potentials (Table 3) for each species were lower on site 3 than on site 5. Midday leaf water potentials decreased through the season (Figure 5) and tended to be lower on site 3 than on site 5. The "A" and "B" water potential values are included on the *Bistorta* and *Caltha* graphs. As at Barrow, leaf water potentials lower than the "A" value were taken as an indication of water stress. *Caltha* appeared to be under some stress at a few points during the season; while *Bistorta* appeared to be under little stress.

Discussion and Conclusions

The relationship between leaf water potential and RSD frequently shows two stages. The first stage consists of a decrease in turgor potential and a concomitant decrease in osmotic potential and may be linear. The second stage is characterized by a rapid decrease in water potential with small increases in RSD, caused by the sorptive forces associated with the solid-liquid interfaces of various cellular components (Slatyer, 1967). Over the range of RSD found in the field, only the first stage was detectable in the six Barrow species and *Bistorta*; however, *Caltha* exhibited both phases.

The differences in the slope of the first phase of the leaf water potential-RSD curve among species is related to the sensitivity of cell turgor to water loss and is interpreted as being related to the cell wall elasticity. Plants with rigid or inelastic cell walls lose turgor more rapidly per unit of water loss than species with more elastic cell walls. Hence, plants with more elastic cell walls will tend to lose more water (develop higher RSD) before stomates close. In general, as one proceeds along a moisture gradient from wet to mesic, cell wall elasticity increases allowing a greater amount of water to be lost before stomatal closure. However,

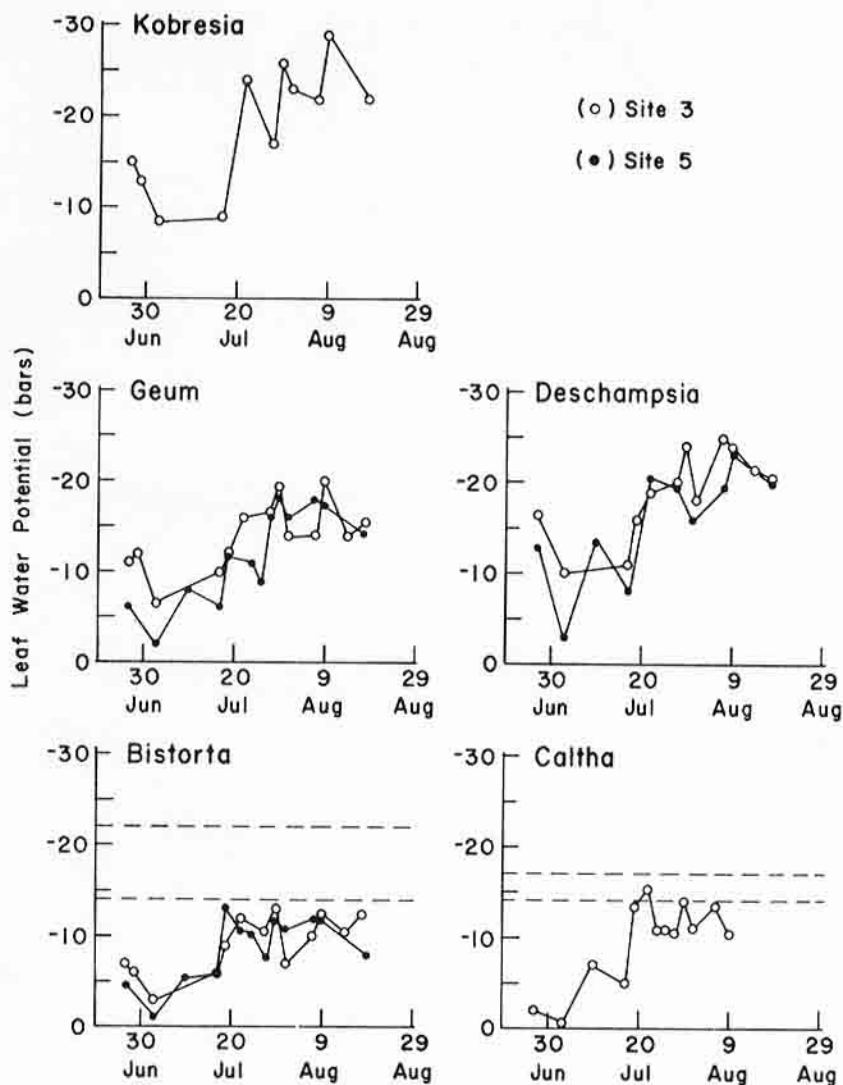


Figure 5. Seasonal courses of midday leaf water potentials of the Niwot species from site 3 (○) and site 5 (●).

the sensitivity of stomatal opening to leaf water content may vary among species due to other factors such as guard cell construction. *Arctophila* shows the greatest rate of change of leaf water potential to RSD. *Dupontia*, *Carex*, *Salix*, *Bistorta*, and *Potentilla* are next. *Eriophorum* and *Caltha* showed the lowest changes in leaf water potential with RSD. However, the species do not fall out in the same order in terms of their RSD at stomatal closure (40 sec cm^{-1} , see Fig. 2). RSD at stomatal closure was 7% for *Arctophila*, 11% for *Caltha*, 13% for

Dupontia, 17% for *Carex*, 19% for *Potentilla*, 20% for *Salix*, 27.5% for *Bistorta*, and 28% for *Eriophorum*.

Perhaps a better method of comparing the species is one which takes into account the shape of the leaf resistance-leaf water potential curve. If we linearize the curve by converting to conductances and compare the first derivatives, the species in order of decreasing sensitivity of leaf resistance to leaf water potential are: (1) *Arctophila*, (2) *Dupontia*, (3) *Caltha*, (4) *Carex*, (5) *Eriophorum*, (6) *Bistorta*, (7) *Potentilla*, and (8) *Salix*. *Caltha* is more like the species from the wet end of the Barrow gradient; while *Bistorta* is more like those from the dry end.

At both Barrow and Niwot, lower leaf water potentials occurred than previously reported. At Barrow, leaf water potentials in the range of -15 to -20 bars occurred during both growing seasons of 1972 and 1973. At Niwot minimum leaf water potentials were -40 bars for *Kobresia*, -23 bars for *Geum*, -17 bars for *Bistorta*, -31 bars for *Deschampsia*, and -17 bars for *Caltha*.

Minimum leaf resistances and cuticular resistances are similar among arctic, alpine, and mesic species in more temperate areas. Root resistances of arctic and alpine species are similar to some agricultural species (Brouwer, 1954; Hay and Anderson, 1972; Dunham and Nye, 1973; Johnson and Caldwell, 1976). The apparent insensitivity of root resistance to soil temperature seen in the Barrow species has been seen in alpine species (McNaughton et al., 1974).

The role of water in limiting production and distributions is complex. Certainly, *Arctophila* and *Dupontia* would be under considerable stress in the alpine environment since their leaf resistances are more sensitive to leaf water potentials than *Caltha*, which is at the xeric end of its distribution at site 5. In the arctic even though some stomatal closure was evident in *Dupontia* in 1972 and in *Arctophila* and *Potentilla* in 1973, it probably did not occur frequently enough to affect the carbon balance of these species by reducing photosynthesis. However, low leaf water potentials are known to affect the mortality and expansion of new leaf tissue in agricultural species (Hsiao, 1973). At present, the effects of low leaf water potentials on these processes in tundra species are unknown.

In the alpine, no stomatal closure was evident in *Bistorta* or *Caltha*, even though 1972 was a dry year. However, the daily courses of water potential from sites 3 and 5 early in the season indicated 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. Later in the season at the peak of drought stress, those species which occur 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 which are 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. It is expected that leaf water potentials of the species at the xeric end of its distribution will frequently be in the position of the leaf resistance-leaf water potential curve where leaf resistances increase rapidly in response to changes in leaf water and that the increased leaf resistances may also restrict production.

In general, plants in both the arctic and alpine may be limited in their distributions by water stress, but, in areas where they grow, water probably does not limit production except in very dry years.

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