

GAS EXCHANGE STUDIES OF FOUR ALPINE TUNDRA SPECIES AT NIWOT RIDGE, COLORADO

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INTRODUCTION

During the past decade several researchers have studied gas exchange characteristics of various alpine tundra plants under field conditions in the Appalachian, Sierra and Rocky Mountains (Billings *et al.* 1966, Scott and Billings 1964, Hadley and Bliss 1964, Bliss 1966, and Mooney *et al.* 1964). Other studies have compared gas exchange characteristics and physiology of alpine tundra plants with their arctic or low altitude counterparts (Mooney and Billings 1961, Mooney 1963, Mooney and Johnson 1965). Extensive field measurements of alpine plant photosynthesis have also been carried out in the Austrian Alps by Moser (1973).

This study was initiated to provide additional information on gas exchange rates of four alpine tundra species (*Kobresia myosuroides* (Vill.) Fiori and Paol, *Deschampsia caespitosa* (L.) Beauv., *Geum rossii* (R. Br). Ser., and *Bistorta bistortoides* (Pursh.) Small) in the central Colorado area.

METHODS

The data reported here were collected at approximately 3500 m elevation on the gently sloping saddle of Niwot Ridge near Boulder, Colorado. Measurements were initiated June 28 and were continued alternately among species until August 20, 1972.

Rates of net photosynthesis and transpiration for whole plants were measured at 5°C increments from 10°C to 30°C with irradiation above 70 mW cm⁻² which was considered to be near or

above saturation. Dark respiration rates were determined at the same temperatures. The measurements were obtained with a Siemens gas exchange cuvette (Koch *et al.*, 1971) and a Beckman differential gas analyzer. Cambridge dew point hygrometers were used to monitor incoming (ambient) and outgoing water vapor concentrations.

Sylvania 300 W "Cool-lux" incandescent lamps and partial solar shading were used to provide the desired irradiation intensity. A thermopile pyranometer within the cuvette was used to monitor irradiation and leaf temperatures were measured with 0.08 mm dia. copper-constantan thermocouples inserted into the leaves.

Leaf areas for *Geum rossii* were estimated from regression relationships of leaf dry weight with leaf area and with leaf length and width. The leaves of *Deschampsia caespitosa* and *Kobresia myosuroides* were treated as simple linear strips with effective widths of .21 and .10 cm respectively. Tracings of the *Bistorta bistortoides* leaves were measured with a planimeter. Most of the above-ground portion of each plant was enclosed in the cuvette.

RESULTS

Net photosynthetic and dark respiration rates of the four species in relation to leaf temperature are shown in Table 1. Each date represents measurements from an individual plant, indicating a substantial shift in photosynthetic rates during the season for *Deschampsia caespitosa* and a lesser one for *Geum rossii* with peak assimilation during mid-season. *Kobresia myosuroides* showed very low photosynthetic rates throughout the study period while *Bistorta bistortoides* exhibited quite high rates on the two dates sampled. The low net photosynthetic rates of *Kobresia* may have been related to an abundance of senescent leaf tissue, a high boundary layer resistance caused by leaf clustering near the base, and mutual shading near the base.

Respiration rates for *Geum* and *Kobresia* appeared to be highest early in the season while the respiration rates for *Bistorta* increased from early to mid-season.

A comparison of transpiration rates (Table 2) exhibited by *Geum* indicates some relationship to the apparent seasonal shift in photosynthetic capacities with a progressive decline and a shift of peak transpiration from about 20°C to about 30°C during the season. *Kobresia* and *Deschampsia*, however, showed little variability in transpiration rate among plants. Transpiration rates of *Bistorta* increased from June to July as did net photosynthesis.

Water vapor diffusive resistances (Table 2) were quite high in most instances. The high resistances were partially due to

Table 1. Net photosynthesis and dark respiration of four tundra species at Niwot Ridge ($\text{mg dm}^{-2} \text{h}^{-1}$).

Species	Leaf Temperature $\pm 1^\circ\text{C}$				
	10	15	20	25	30
Net Photosynthesis					
<i>Deschampsia caespitosa</i>					
27 June	0.78	- 0.12	- 0.17	-	-
20 July		10.70	11.77	10.70	5.63
3 Aug	3.47	3.76	3.68	3.10	2.60
17 Aug	1.35	0.79	0.96	-	-
<i>Kobresia myosuroides</i>					
12 July	0.52	0.57	0.77	0.51	-
26 July	0.78	0.61	0.39	0.10	- 0.37
8 Aug	0.11	0.06	1.15	-	-
<i>Geum rossii</i>					
9 July	6.37	6.60	3.36	2.56	2.06
28 July	6.34	6.48	7.11	5.42	-
13 Aug	4.47	5.38	5.61	4.59	3.14
23 Aug	0.39	0.09	0.02	- 0.21	-
<i>Bistorta bistortoides</i>					
29 June	7.20	8.41	8.43	8.03	7.74
15 July	16.54	19.81	17.27	11.92	10.74
Respiration					
<i>Deschampsia caespitosa</i>					
27 June	0.39	0.59	0.88	1.16	1.50
20 July	- .69	-	-	1.88	2.38
3 Aug	0.42	0.57	0.75	1.02	-
<i>Kobresia myosuroides</i>					
12 July	0.78	1.15	1.25	-	-
26 July	0.25	0.38	0.50	0.71	0.93
<i>Geum rossii</i>					
9 July	0.92	1.40	2.04	2.84	3.86
28 July	0.63	0.96	1.32	1.79	2.39
13 Aug	0.94	1.03	1.29	1.66	2.22
<i>Bistorta bistortoides</i>					
29 June	1.03	1.21	1.95	2.84	-
15 July	1.56	2.34	3.99	4.83	6.54

Table 2. Transpiration ($\text{mg dm}^2/\text{hr}$) and total transpiration resistances (sec/cm) of four tundra species at Niwot Ridge

Species	Leaf Temperature $\pm 1^\circ\text{C}$				
	10	15	20	25	30
<i>Deschampsia caespitosa</i>					
27 June	30	-	-	-	-
20 July	-	380	250	442	706
3 Aug	149	271	417	589	742
17 Aug	133	224	326	-	-
<i>Kobresia myosuroides</i>					
12 July	68	-	269	296	364
26 July	81	82	130	186	380
8 Aug	63	122	226	-	-
<i>Geum rossii</i>					
9 July	391	644	749	689	537
28 July	59	201	540	681	-
13 Aug	61	69	306	501	589
23 Aug	35	-	144	175	-
<i>Bistorta bistortoides</i>					
29 June	275	338	525	793	182
15 July	270	649	1190	2060	2275
Total Transpiration Resistance					
<i>Deschampsia caespitosa</i>					
27 June	54.9	-	-	-	-
30 July	-	4.7	4.1	8.9	8.3
3 Aug	8.3	5.9	6.5	8.3	8.3
17 Aug	10.0	10.6	11.2	-	-
<i>Kobresia myosuroides</i>					
12 July	20.1	-	13.0	17.7	20.1
26 July	19.5	26.6	27.1	31.3	21.8
8 Aug	28.3	21.8	17.1	-	-
<i>Geum rossii</i>					
9 July	-	1.3	2.9	5.9	13.0
28 July	25.4	11.8	5.9	6.5	-
13 Aug	20.6	27.7	9.4	8.8	11.8
23 Aug	58.4	-	27.7	36.0	-
<i>Bistorta bistortoides</i>					
29 June	9.4	7.1	5.9	5.9	56.0
15 July	3.5	3.5	1.8	-	0.6

mechanical limitation of the system which prevented adequate ventilation rates. This problem was compounded in the case of *Kobresia* by poor circulation among the densely clustered leaves.

DISCUSSION

The rapid shift in net photosynthetic rates during the growing season has been observed by other researchers. By harvesting techniques Billings and Bliss (1959) found that plants growing in an alpine snowbank environment exhibited peak daily growth rates soon after release from the snow cover with rates then declining erratically during the remainder of the season. However, as pointed out by Hadley and Bliss (1964) and Bliss (1966) much of the early growth of alpine tundra plants is at the expense of stored energy reserves causing high respiratory and low net photosynthetic rates early in the season.

With the initiation of this study on about July 1, the early growth period had already occurred; and, in the case of *Kobresia*, perhaps even peak photosynthetic rates had passed. The area had been free of snow long enough for all four species to be experiencing some effects of water stress.

Peak photosynthetic data collected by a ^{14}C technique (Unpublished data of D. Johnson) during the same season indicate much higher rates for *Kobresia* and *Deschampsia*. This difference in rates, however, might be largely accounted for by the differences in techniques. The ^{14}C method involved higher illumination of a single leaf sample resulting in near optimum conditions for net photosynthesis.

The relatively small changes in leaf resistance and dark respiration throughout the season for *Deschampsia* suggest that the decline in net photosynthetic rates for this species might be related to a biochemically-based decrease in gross photosynthesis. *Geum*, on the other hand, exhibited an increasing leaf resistance throughout the season. The last *Geum* plant, however, was clearly in an advanced stage of senescence and likely possessed little photosynthetic capability in addition to having a high leaf resistance.

Billings *et al.* (1966) reported substantially higher photosynthetic and respiration rates for *Geum turbinatum* (*G. rossii*) than we observed under comparable conditions on a similar date. Scott and Billings (1964) observed respiration rates for *Geum* from the Medicine Bow Mountains almost double those reported here, but their photosynthetic response data were quite comparable to what we observed for the species. In the case of *Deschampsia*, also from the Medicine Bow Mountains, their respiration rates are about three times those measured in this study while their photosynthetic rates lie between our July 20 and August 3 determinations.

The *Deschampsia* plants we examined, displayed peak net photosynthetic rates below or near 20°C. These determinations involved considerable respiratory tissue as well as the predominantly photosynthetic leaves. Thus, the photosynthetic temperature optima for *Deschampsia* agree reasonably well with the somewhat higher temperature optima (25-30°C) found by Tieszen and Helgager (1968) for *Deschampsia* plants (Hill reaction) from a nearby area.

The respiration rates reported here for *Bistorta* are substantially higher than those reported by Mooney (1963) for a subalpine population. This agrees with the generalization that alpine plants tend to have higher metabolic rates than do their lower altitude relatives.

The data reported here are for individual plants with no replication at each point in the season. As pointed out by Hadley and Bliss (1964) there is a high degree of variability among gas exchange rates of different individuals within a species and even among shoots of a given plant.

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