

Studies on evapotranspiration and energy budgets on Truelove Lowland

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Introduction

The measurement of evapotranspiration and the determination of energy budgets under various environmental conditions may help to explain how a plant is adapted to maintain itself in a harsh environment. Both arctic and alpine tundra species are exposed to harsh environments and Bliss (1971), Savile (1972), and Courtin and Mayo (1975) have discussed some of the plant strategies that ensure growth and development under such conditions.

In the past only a limited amount of work has been done characterizing the physical and physiological responses of arctic plants to their environment with respect to partitioning of absorbed radiation and retention of water in xeric sites (Ahrnsbrak 1968, Romanova 1971, Miller and Tieszen 1972, Weller and Cubley 1972, Haag and Bliss 1974).

It is important that energy budget studies accompany those of water balance, since plant adaptations for water conservation may have far reaching effects on the overall energy regime of a plant community. Plant adaptations to water deficit, therefore, are limited to some extent, because a balance must be reached between the minimum rate of water loss possible and the maximum leaf temperature that can be tolerated.

The aims of this study were: (1) to determine the energy budgets of the two dominant plant communities in this high arctic ecosystem; (2) to study the plant-soil-water relations of plant communities at the ends of a soil moisture gradient; and (3) to explore the ecological implications of presumed adaptations to environmental conditions.

Two sites, a raised beach and a meadow, were chosen for intensive study as they represented the two dominant vegetation types on Truelove Lowland (Bliss 1972). Soils of the raised beach were coarse textured and ranged from regosols to brunisols (Walker and Peters this volume). The general microtopography and plant community pattern of this site have been described by Svoboda (this volume). The meadow site had a Fibric Organic soil (Walker and Peters this volume), and a high water table maintained by the impervious permafrost below. Plant community pattern and general site characteristics are given by Muc (this volume).

Owing to differences in drainage the sites represented the ends of a soil moisture gradient, and the plant communities reflected this gradient. Cushion plants were the dominant vascular plants on the raised beach, while upright sedges dominated the meadow. Since neither site had a homogeneous plant

cover, it was necessary to subdivide each into a number of microsites based upon differences in floristics and water and energy relations. Five microsites comprised the raised beach: (1) vascular plants as represented by *Dryas integrifolia*; (2) crustose lichens; (3) fruticose lichens; (4) fine textured unvegetated soil; and (5) coarsely textured unvegetated soil ($20\% < 2\text{mm}$). The meadow consisted of three microsites: (1) vascular plants (*Carex stans* with an understory of moss); (2) moss alone (mainly *Drepanocladus brevifolius*); and (3) shallow pools of water.

Energy budget

A description of the energy budget shows the relative importance of each method of dissipating absorbed incoming radiation not used in photosynthesis. Dissipation of energy from the beach ridge and meadow is important as it represents a loss of energy from the ecosystem and relates to the overall study of tracing energy flow through the ecosystem.

Plant photosynthesis utilizes a maximum of 2% of the total energy received (Grable et al. 1966) and the organism must be able to dissipate the remaining energy in order to maintain leaf temperatures below the thermal death point. Equation (1) represents algebraically the partitioning of absorbed or net radiation (R_n) for any surface (Gates 1965).

$$R_n = LE + H + G + M \quad (1)$$

where L is the latent heat of vaporization (580 cal g^{-1}); E, rate of water loss ($\text{g cm}^{-2} \text{ min}^{-1}$); H, sensible heat flux; G, soil heat flux, and M, plant metabolic energy. The last is only applicable to plant surfaces. The units of H, G, M, and R_n are $\text{cal cm}^{-2} \text{ min}^{-1}$.

Methods and materials

A Net Radiometer installed at a height of 1 m integrates absorbed radiation over a circular area 10 m in diameter (Reifsnyder and Lull 1965). In areas where there is great heterogeneity in surface characteristics because of a mosaic of microsites, it was important to determine net radiation of each microsite to permit projection of the data to a much larger area. Where microsites were small (often less than 20 cm in diameter), R_n had to be determined indirectly. This was achieved using a Funk Net Radiometer with a black body cup attached to the lower surface. (See Addison 1973.)

Although five microsites comprised the beach ridge, the study of the beach ridge energy relations only required that three be considered. The two lichen microsites were combined as were the two unvegetated soil surfaces to achieve consistency with the work of other researchers who had confined their studies of plant cover at the beach ridge to three components: vascular plants, lichens, and unvegetated soil.

The surface temperatures of both the black body cup and the microsites were measured with copper-constantan thermocouples connected through a cold compensating junction and an automatic stepping switch to a potentiometric millivolt recorder.

Good physical contact between thermocouple and surface is necessary to measure surface temperature accurately. Thermocouples were glued to small pebbles, threaded through lichen thalli and moss stems, and mounted on

leaves with thermocouple clips. The leaf thermocouple clip was a modification of that used for Douglas Fir (*Pseudotsuga menziesii*) by Fry (1965). Five thermocouples connected in parallel were used to estimate the mean surface temperature of each microsite.

Soil energy flux (G) was measured with soil heat flux plates (3×5 cm) placed 1 cm below and parallel to the soil surface. These plates measured the rate of energy transfer through the soil beneath *Dryas*, *Carex*, lichen, and water surfaces. It was assumed that the insulative capacity of lichens was negligible because of the sparse cover and, therefore, soil energy flux beneath bare soil and lichens was assumed to be similar. It was assumed also that the soil heat flux beneath a moss canopy was the same as that beneath *Carex* and moss together. At the vascular plant microsites, the metabolic energy flux (M) was assumed to be 2% of global radiation (R_t). Sensible heat flux (H) from all microsites was calculated using equation (1), since R_n , LE , G and M were known.

Results and discussion

Longwave radiation (L_d) comprised over half of the total incoming radiation on 17 and 18 July, mainly as a result of dense clouds during early 18 July (Fig. 1), and the presence of a rock outcrop that emitted radiation to the site. Fig. 1 also shows that longwave radiation compensated for reductions in global radiation (R_t) caused by light cloud. There were sudden drops in shortwave flux at 0800 hr on 17 July and at 1200 hr on 18 July. At those times there was a corresponding increase in longwave flux and a resultant smooth curve of total incoming radiation.

Cushion Plant-Lichen community (Raised Beach)

Most of the energy absorbed by the vascular plants on 17 and 18 July was dissipated as sensible heat flux (86%) rather than by either latent heat flux (11%) or soil heat flux (3%). This last term was very small and has been excluded from Fig. 2. There was a reduction in latent heat flux at or shortly after 1200 hr on both days. This drop in latent heat flux was probably a result of "midday stomatal closure" caused by leaf water deficit. This deficit was created by transpiration exceeding the rate of water uptake by the roots. After the plant recovered, the stomata reopened and transpiration increased.

Similar curves for a lichen cover are shown in Fig. 3. Since lichens have no structures controlling water loss, latent heat flux (29%) of lichens was greater than that of vascular plants. Sensible heat flux (64%), however, was the major method of energy dissipation. The cover of lichens on the raised beach (25%) was sparse and so there was little resistance to heat transfer into the ground. The lichen cover therefore had a much larger soil heat flux (7%) than did *Dryas* (3%).

Net radiation of lichens on 17 July was substantially higher than that of *Dryas* during the 6 hr period spanning 1200 hr. The explanation for the difference lies in longwave radiation leaving the two surfaces. The emission of longwave radiation from any object is temperature dependent and, since *Dryas* was 30 °C warmer than the lichens at this time, more radiant energy was emitted by *Dryas*. This resulted in a greater amount of incoming energy remaining at the lichen surface and hence, greater net radiation. When surface temperatures of the two microsites were similar (e.g., 1400 hr on 17 July), net radiation was the same for both surfaces.

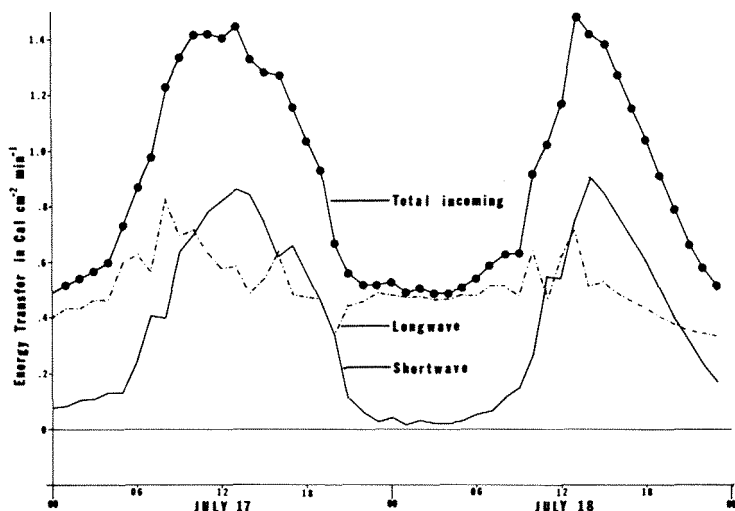


Fig. 1. Total incoming radiation (all wavelengths) and its longwave and shortwave components on 17 and 18 July, 1972.

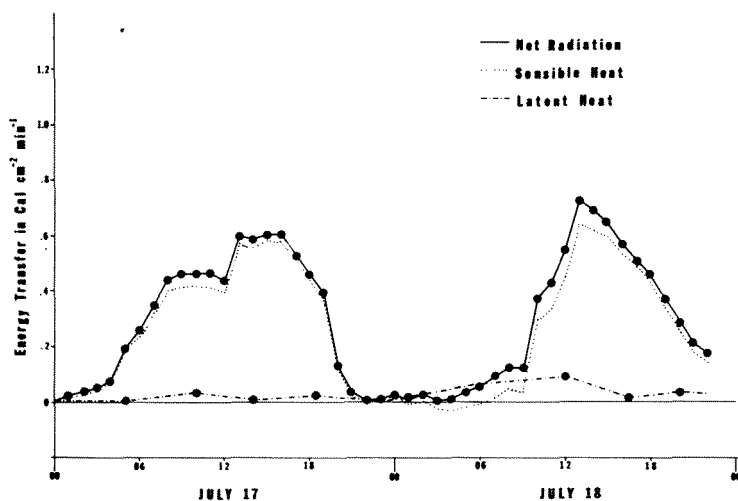


Fig. 2. Net radiation and its components for *Dryas integrifolia* on 17 and 18 July, 1972 (raised beach).

The various fluxes that comprise bare soil R_n lay between those of *Dryas* and lichen microsities. Most absorbed energy was dissipated as sensible heat flux (79%) whereas only 15% was lost as latent heat flux and 6% as soil heat flux. Since the surface temperature of unvegetated soil was similar to that of lichen thalli, emitted longwave radiation was similar for both microsities as was R_n .

Dryas leaf temperature varied much more than did the temperature of either of the other two microsities at the raised beach. On 17 July leaf

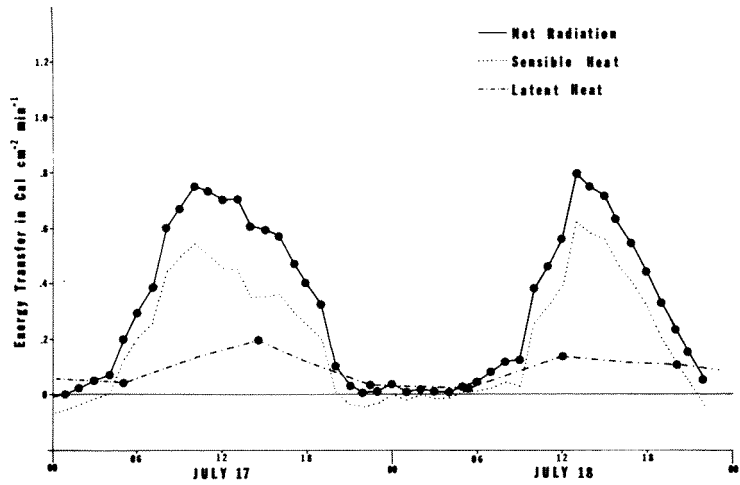


Fig. 3. Net radiation and its components for a lichen surface on 17 and 18 July, 1972 (raised beach).

Table 1. Generalized energy regime of the raised beach microsites under different incoming radiation conditions.

Microsite	I $ly\ min^{-1}$	R_n $ly\ min^{-1}$	LE $\% R_n$	H $\% R_n$	G $\% R_n$
17 July (sunny)					
Vascular Plants	0.952	0.304	4.9	92.2	2.9
Lichens	0.952	0.351	29.1	61.1	9.8
Unvegetated Soil	0.952	0.337	13.2	76.6	10.2
24-25 July (cloudy)					
Vascular Plants	0.609	0.089	24.3	73.9	1.8
Lichens	0.609	0.094	34.2	54.3	11.5
Unvegetated Soil	0.609	0.100	25.0	64.2	10.8

temperature remained above 45°C for three hours. This value is within the range of 45°C to 55°C given by Clum (1926) as the thermal death point of many plant species. The temperature recorded for *Dryas* was a mean of five sensors placed at the centre and four cardinal points of the cushion. Since these were mean temperatures and some of the leaves received more radiation than others (because of their orientation), it is inevitable that some were warmer than the mean. Several days of each year have similar levels of radiation and low wind speed but, nevertheless, the plant had no signs of heat kill.

Each microsite of the raised beach showed a similar diurnal pattern of energy dissipation on both sunny (17 and 18 July) and cloudy (24 and 25 July) days. There were, however, significant differences at all microsites between the two types of days in the ratio of net to incoming radiation. It can be seen from Table 1 that with a drop in incoming radiation (I), there was a greater reduction in R_n . The ratio of R_n to I dropped from 0.34 to 0.15 on cloudy days. Because of the much reduced heat load during cloudy days, it

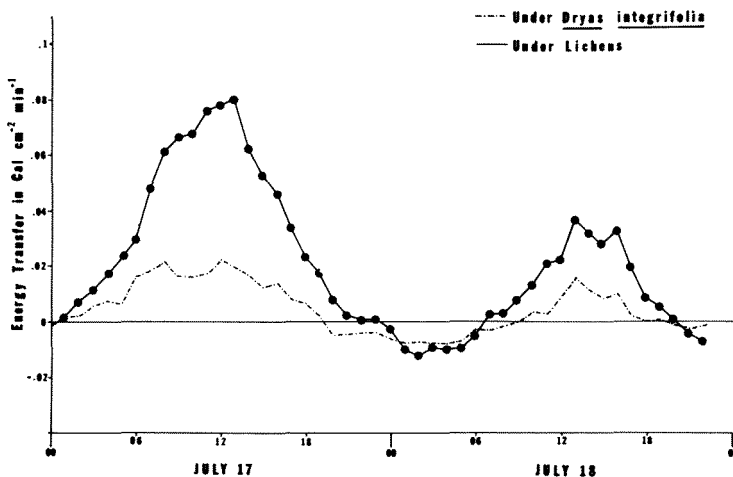


Fig. 4. Soil heat flux beneath *Dryas integrifolia* and lichens during 17 and 18 July, 1972 at the raised beach.

was possible for each microsite to dissipate a greater proportion of absorbed energy by latent heat flux (LE). This resulted in less energy dissipated by the relatively inefficient process of sensible heat flux (H), and hence, much lower surface temperatures on cloudy days than on sunny days at each microsite. There was less variation in R_n among the microsites on dull days than on bright ones, presumably as a result of similar surface temperatures on the dull days.

In all surfaces studied, soil heat flux (G) represented only a small part of energy dissipated. There was, however, a marked difference between soil heat flux beneath vascular plants (*Dryas*) and that beneath a lichen cover (Fig. 4). The very low soil heat flux beneath *Dryas* resulted from a high insulative capacity of the cushion growth form. Other raised beach species such as *Salix arctica* on the other hand, have been shown to have highly fluctuating near-surface soil temperatures as a result of a high soil heat flux (Warren-Wilson 1957). Lichen cover on the raised beach was sparse and offered very little resistance to transfer of energy into the ground. Surface insulation by cushion plants works in both directions and resulted in soil heat flux beneath lichens being greater than that beneath *Dryas* during the day and less during the "night" hours (i.e., 0000 to 0600 hr on 18 July).

Hummocky Sedge-Moss Meadow

Soil heat flux beneath a *Carex* community and that beneath a shallow pool of water are presented in Fig. 5. *Carex* intercepted and dissipated much of the incoming energy before it reached the ground surface and reduced G by 50%. The shallow active layer at this site resulted from insulation of the surface by the plants retarding the melt of frozen soil beneath. The soil energy flux beneath a shallow pool of water was always positive because of the steep gradient between warm surface water and the frost table only 25 cm below.

Water was not limiting at all microsites at the meadow, and all surfaces lost over 40% of absorbed energy through latent heat flux (Table 2). From this it seems that the *Carex* microsite was dominated in water loss by the moss understory. There was, however, 10% more energy dissipated as LE at

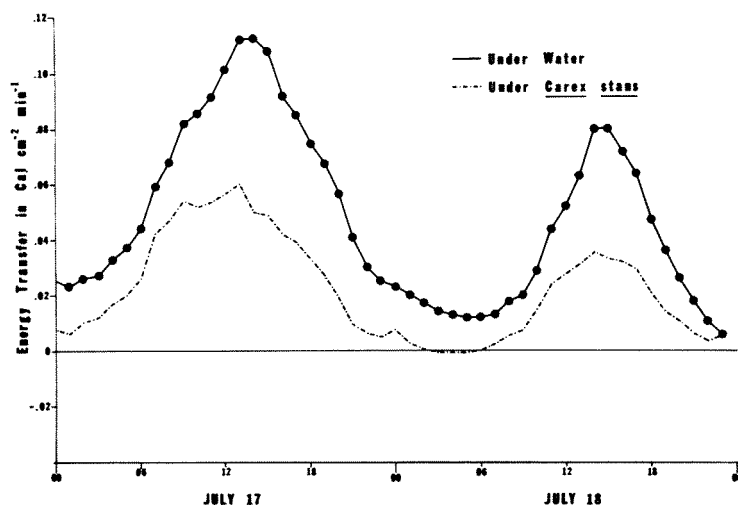


Fig. 5. Soil heat flux beneath *Carex stans* and water during 17 and 18 July, 1972 at the meadow site.

Table 2. Generalized energy regime of the hummocky sedge-moss meadow microsites under different solar radiation conditions.

Microsite	I $ly\ min^{-1}$	R_n $ly\ min^{-1}$	LE % R_n	H % R_n	G % R_n
17 July (sunny)					
Vascular Plants	0.952	0.368	54.6	37.0	8.4
Moss	0.952	0.387	44.0	48.0	8.0
Water	0.952	0.385	43.7	40.0	16.3
24-25 July (cloudy)					
Vascular Plants	0.609	0.110	49.6	40.6	9.8
Moss	0.609	0.117	54.8	36.1	9.2
Water	0.609	0.119	83.6	-4.0	20.4

the *Carex* microsite as compared with that of moss alone on 17 July. This was a very small difference when related to the substantial increase in surface area (2.5x) but did show that the vascular plants added a component to the energy dissipation at this site. At all three microsites the peak of latent heat flux corresponded approximately to the time when relative humidity was lowest and surface temperatures highest.

Energy dissipation on dull days (24 and 25 July) at all meadow microsites was similar to that on a clear day (17 July). The meadow microsites followed those at the raised beach showing a reduction in the ratio of R_n to I and an increase in the proportion of R_n dissipated as latent heat flux on cloudy vs. sunny days (Table 2). The great differences in the water microsite are owing to a change in the instrument to measure LE .

Both sites general

Figure 6a represents diagrammatically the energy regime of the entire raised beach on 17 July, 1972. The beach ridge had a cover of 25% vascular plants

Table 3. Net radiation on sunny days at six arctic sites.

Net Radiation (cal cm ⁻² min ⁻¹)	Site	Observer
0.342	Meadow, Devon Island, N.W.T.	Addison
0.310	Beach Ridge, Devon Island, N.W.T.	Addison
0.264	Meadow, Point Barrow, Alaska	Weller & Cubley
0.262	Lichen Mat, Pelly Lake, N.W.T.	Ahrnsbrak
0.224	Lichen Mat, Snowbunting Lake	Ahrnsbrak
0.178	Lichen Mat, Curtis Lake, N.W.T.	Ahrnsbrak

(Svoboda this volume), 25% lichens (Richardson and Finegan this volume) and 50% unvegetated soil. Longwave radiation (L_w) was the most important method of dissipating incoming energy. This observation concurs with that of Mellor et al. (1964) for a wide range of plant species under controlled environments. Net radiation (R_n) of the community was dissipated mainly by sensible heat flux (H). Sensible heat flux was five times greater than latent heat flux (LE) and ten times that of soil heat flux (G).

The meadow was comprised of 70% vascular plants with an understory of moss, 20% moss alone, and 10% standing water. Latent heat flux accounted for over 50% of the net radiation (Fig. 6). The meadow community had a 10% higher R_n than did the raised beach, presumably because of the small amount of reflected shortwave radiation (R_i) and lower emissions of longwave radiation resulting from lower surface temperatures. This compares closely with R_n values presented by Courtin (1972) for these same communities at a similar time in 1971. Soil heat flux at the meadow was slightly larger, comprising 8% on R_n as compared to 5% at the raised beach.

Shortwave incoming radiation on 17 and 18 July was comparable with reported values from Snowbunting Lake, Curtis Lake, and Pelly Lake, N.W.T. (Ahrnsbrak 1968) and from Barrow, Alaska (Weller and Cubley 1972) but net radiation of both sites on Devon Island was higher than any of these other sites (Table 3).

The major cause of the difference between the Devon sites and those studied by Ahrnsbrak (1968) and Weller and Cubley (1972) appears to be in the higher amount of longwave radiation. Large rock outcrops are located close to both sites and, since these stand above the surface, some longwave radiation received was from the rocks. This increased total incoming radiation resulted in higher values of net radiation than would be expected from the incoming shortwave radiation measurements.

In general, the energy regime of the beach ridge reflects the nature of its substrate (a dry gravel) and over 65% of the energy that strikes this surface is either reflected or reradiated immediately upon receipt. The beach ridge is characterized by its cover of lichens and the presence of large areas that are devoid of vegetation. The energy regime of this site also reflects this lack of vegetation because it responds to changes in radiation load in a similar manner to that of the bare soil microsite alone.

The *Carex* microsite typifies the meadow mosaic pattern, a system in which over 50% of R_n is dissipated as LE .

Water relations

Water can become limiting to growth whenever the ratio of precipitation to evaporation is low or where there is rapid drainage or runoff. Both of these conditions exist on raised beaches where *Dryas integrifolia* is one of the

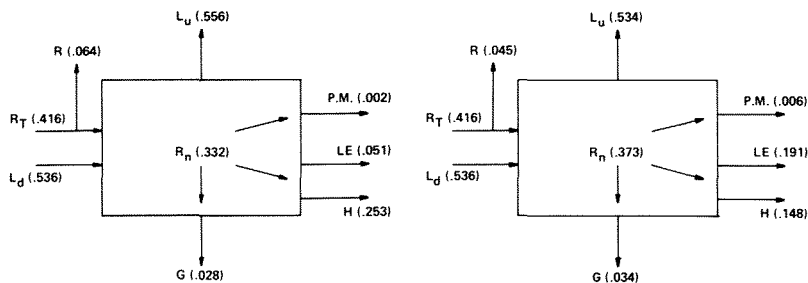


Fig. 6. Energy regime of the raised beach (a) and hummocky sedge-moss meadow (b) intensive study sites under high insolation (17 July, 1972). Units are $\text{cal cm}^{-2} \text{ min}^{-1}$.

dominant plant species (Svoboda this volume). An understanding of how *Dryas* is adapted to withstand water deficit is only possible by examining the water regime of the soil-plant-atmosphere continuum under various environmental conditions and in the light of the energy regime of the surface.

One of the most important terms in the soil-plant-atmosphere continuum is the rate of water loss from a vegetated surface to the air. This process consists of transpiration from the leaves and evaporation from the soil around the plant. Both of these terms are important when describing water relations of a plant community as both reduce the amount of water that is available to the plant. Various methods of measuring evapotranspiration have been reviewed by Kohnke et al. (1940), Pelton (1961), Van Bavel (1961), Courtin and Bliss (1971), and Mukammal (1971). These methods include the use of potometers, evaporimeters, Bowen Ratio, aero heat method, sod blocks, and lysimeters.

Not only is it important to determine the rate of water loss from a plant community, but it is also necessary to describe the water status of the various parts of the continuum. When water is in the gaseous state, it moves down gradients of vapour density ($\text{g H}_2\text{O cm}^{-3}$) but when it is in the liquid state, it moves in response to a gradient in water potential (ψ_w). Water potential is a function of the difference in chemical potential between the water under consideration and pure free water at the same temperature and pressure.

Methods and materials

In this study a lysimeter was developed that could be installed within the active layer of arctic soils (Addison 1973). The active layer in hydric meadow areas can be as shallow as 20 cm, and therefore, even the miniature hydrostatic lysimeter described by Courtin and Bliss (1971) was too large to be of use.

Four lysimeters were installed at each site and the soil surface of two was sealed with silicone rubber to prevent evaporation from soil around the plant. The sealed pots gave a measurement of transpiration while the open ones gave evapotranspiration.

Sod blocks were used at each site to supplement lysimetric data and to determine evaporation rates of non-vascular plant surfaces. Sod blocks were the same size as the lysimeter pots (8.25 cm in diameter and 11.5 cm deep) and were positioned in a similar manner with the top flush with the soil surface. Measurements were made by removing sod blocks and weighing them on a triple beam balance ($\pm 0.1 \text{ g}$).

The rate of water loss from any surface is directly proportional to its evaporative surface area, so to obtain comparable data from each of the microsites, the surface area of each was measured. Leaf area of vascular plants was determined using the Ballotini glass ball technique of Thompson and Leyton (1971). Since water loss from vascular plants is almost entirely through their stomata, the evaporative surface may be considered as that area where stomata are present. *Carex stans* is amphistomatous and therefore, the evaporative leaf area was the sum of both surfaces. The leaves of *Dryas integrifolia*, on the other hand, have stomata on only the abaxial surface. This surface is pubescent, however, and it was not possible to coat it with glass balls. As a result, the adaxial surface was measured and it was assumed that this area was the same as that of the lower surface. The area of the non-vascular plant surfaces was measured by casting the entire surface of the sod block in silicone rubber and determining the area of the cast with the Ballotini glass ball technique.

Leaf water potential was measured with a Wescor chamber psychrometer and a microvoltmeter that followed the method of Spanner (1951). Soil water potential was measured by a similar method using Wescor soil psychrometers and the same meter. The chamber and soil psychrometers were calibrated with sodium chloride solutions of known water potential.

Plant samples were collected in the field and brought into the laboratory in small sealed bottles. Care was taken to ensure that the bottles were completely full so that water loss from the tissue was minimized. Three readings of the chamber psychrometer were taken for each sample, 10 min apart and after an initial 40 min equilibration time. The soil psychrometers were soaked in water for 24 hr and installed in the raised beach one week in advance of measuring to allow equilibration with the soil.

Results and discussion

It is seen from Fig. 7 that availability of water, as indicated by the water potential of the leaf tissue, limited the rate of transpiration of *Dryas* at the raised beach. Periods of precipitation were accompanied by an increase in both transpiration and leaf water potential. As the soil dried, both parameters decreased until the soil was again replenished by rain. Fig. 8 shows that this relationship did not hold for the *Carex* microsite at the meadow. Precipitation had little or no effect on either of the measured parameters, presumably because of the high water content in the soil (>400% ODW). Variations in transpiration at the meadow were probably a result of the natural variation in aboveground environmental conditions such as radiation load, relative humidity and wind speed.

Cushion Plant-Lichen community (Raised Beach)

Microsites at the raised beach differed greatly from each other in evaporation rate. Table 4 shows that although there was more water lost from crustose lichens than from fruticose lichens, the effect of crustose cover on water loss was small when its rate was compared with that of adjacent bare soil. Fruticose lichens, on the other hand, had an evaporation rate of almost twice that of adjacent bare soil. Water loss from all non-vascular plant microsites was greater than that from *Dryas*.

The main reason why the two lichen covers react differently to the evaporative demand of the air probably lies in their morphology. The vertical

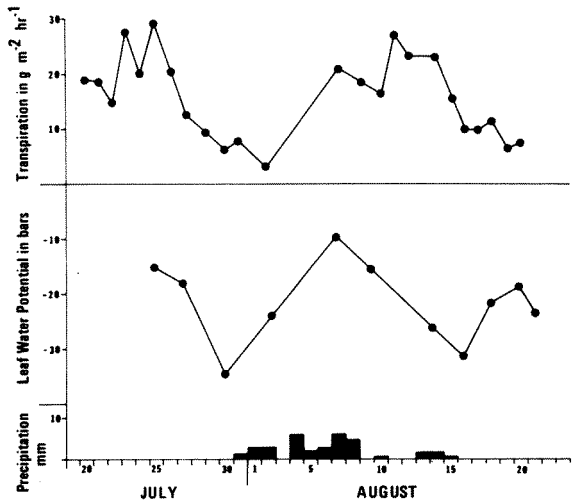


Fig. 7. Transpiration and leaf water potential of *Dryas integrifolia* and precipitation at the raised beach (1971).

Table 4. A comparison of the water status at the raised beach microsites (15 July to 23 August mean, 1971).

Site	Major flora	Soil moisture	Rate of evaporation ($\text{g m}^{-2} \text{hr}^{-1}$)	
		0-10 cm (% ODW)	Vegetated surface	Non-vegetated surface
Mesic	<i>Dryas</i>	23.81	15.4	44.3
Mesic	Crustose Lichens	23.81	43.6	44.3
Xeric	Fruticose Lichens	1.1	32.4	19.3

and branching nature of fruticose lichens resulted in a 16% larger evaporative surface per unit area of microsite than that of the coarse bare soil. A higher evaporation rate was observed for these lichens during the entire summer. The crustose lichens, on the other hand, formed a comparatively smooth surface closely associated with the ground and had a slightly smaller surface area than did the fine bare soil microsite. This suggests that evaporation from bare soil might always be greater than that from crustose lichens but Fig. 9 shows that this was not the case. When the surface was wet, the larger surface area of the bare soil resulted in a greater evaporation rate but, when the surface was dry, the reverse was true. Under dry conditions, evaporation from bare soil must have been from within the soil rather than from its surface. Since evaporated water would have had to move as vapor through the soil pores to the surface before it could be lost, the water transfer pathway was lengthened. This lengthening of the pathway was probably the cause of the reduction of the evaporation rate at the fine bare soil microsite during dry periods. In the case of crustose lichens evaporation was lower than the bare soil during the wet periods and therefore more water remained in the soil during these periods. When the lichens started to dry, the retained water was available to the plant.

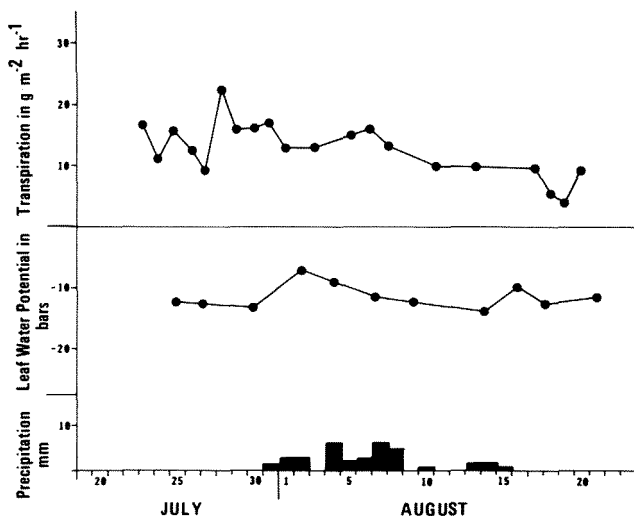


Fig. 8. Transpiration and leaf water potential of *Carex stans* and precipitation at the hummocky sedge-moss meadow (1971).

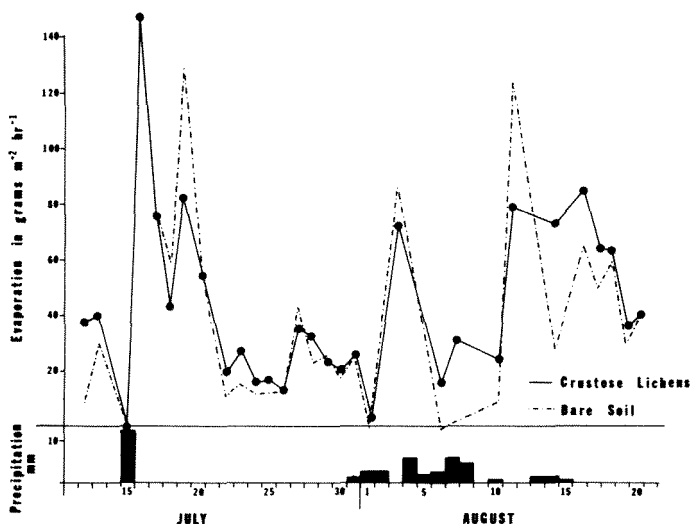


Fig. 9. Seasonal march of evaporation from crustose lichens and bare soil at the raised beach (1971).

The mesic and xeric unvegetated microsites differed greatly with respect to soil moisture, evaporation rate, and net seasonal water flux (Table 4). The probable reason for these differences lies in the soil texture of the two areas. The mesic site had 60% of particles less than 2 mm in diameter whereas the xeric site had only 1.3%. This lack of fine material at the xeric site led to deep percolation of water, rapid surface drying and, ultimately, to a drier soil, less water loss, and a downward net seasonal water flux.

Fig. 10 shows that *Dryas* maintained a water potential gradient between

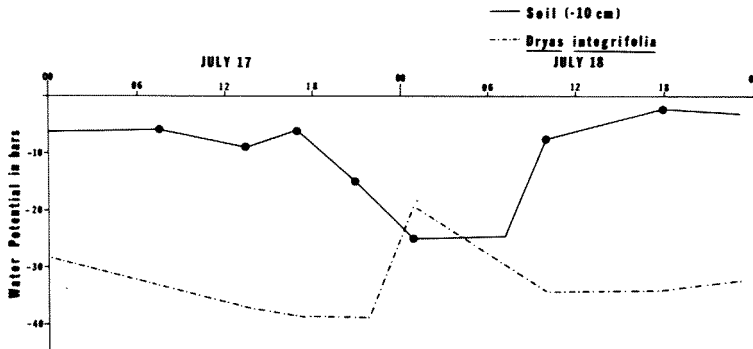


Fig. 10. Soil and leaf water potential during 17 and 18 July, 1972 at the raised beach.

its leaves and the soil of about 25 bars for most of the period presented. Because of stability of soil moisture and low transpiration rates of *Dryas*, the plant had a relatively constant leaf water potential (-35 bars) for most of the period. Such a low water potential was not atypical for *Dryas* and was similar to the seasonal mean (-32 bars). The seasonal mean soil water potential was -20 bars and hence there was usually a substantial gradient through the plant (i.e., 12 bars).

The dramatic increase in leaf water potential (Fig. 10) corresponded to the beginning of precipitation and it is presumed that the measurement of leaf water potential was in error owing to surface moisture on the leaves. Water on the leaf surface evaporated freely as it was not subjected to internal leaf resistances to water vapor transfer that control transpiration. As a result of surface evaporation, there was a much higher latent heat flux and lower leaf temperatures on 18 July than on 17 July.

In general, the four non-vascular plant microsites at the raised beach lost water faster than *Dryas*. These microsites, therefore, are primarily responsible for the dry conditions but temperature gradients in soil are also of importance. Since vapor pressure is temperature dependent, there was a gradient in vapor pressure established from the warm surface to the permafrost resulting in a downward water flux. Extremely dry conditions on the beach ridge are characterized by fruticose lichens that increase evaporation from the soil and coarse bare soil that permits rapid drainage. In areas where the texture of the soil is finer, more moisture is held in the upper layers and crustose lichens predominate.

Hummocky Sedge-Moss Meadow

Carex stans at the meadow had a low transpiration rate even though it was rooted in a soil that was saturated with water. The explanation for this appears to lie in reduction of root permeability to water as a result of cold and poorly aerated soil. This reduction limited the flow of water to the leaves and occasionally caused water potentials as low as -40 bars and stomatal closure.

Evapotranspiration from the *Carex* microsite was $72.2 \text{ g m}^{-2} \text{ hr}^{-1}$ over the summer of 1971 (15 July to 20 August) but of that, only 25% was contributed by the *Carex* even though it represented 75% of the evaporative surface area. In general, *Carex* reduced evaporation from the moss and microsites with moss alone lost $79.2 \text{ g m}^{-2} \text{ hr}^{-1}$. Evaporation from standing

Table 5. Evapotranspiration from the intensive meadow and intensive raised beach site for 1971-1973. Figures for 1972 and 1973 are estimates.

Site	Seasonal water loss ($\text{g m}^{-2} \text{hr}^{-1}$)		
	1971	1972	1973
Meadow	73.1	83.3	89.0
Raised Beach	33.5	38.3	41.0

water averaged $67.4 \text{ g m}^{-2} \text{hr}^{-1}$ in 1971 and the difference between this site and the moss resulted from the larger surface area of the moss. Moss surface area was 2.5 times that of standing water relative to a plane of equal perimeter, but when the moss was saturated only a few stems protruded above the water resulting in only a slightly greater surface area. These conditions were maintained for most of the summer. Moss and standing water, therefore, are responsible for most of the water loss from the meadow and there appears to be little biological control on evapotranspiration at this site.

On a seasonal basis, the meadow lost slightly over two times the amount of water as the raised beach ridge (Table 5). Seasonal averages for 1972 and 1973 are estimates based on the energy relations of the two sites during 1971 and 1972 and on radiation data from Courtin and Labine (this volume). It should be noted that there was very little difference in evapotranspiration rate (E) among the years and most of the great difference in E between 1972 and 1973 as shown by Rydén (this volume) was a result of a much longer snow free period (45 days in 1972 vs. 76 days in 1973).

Plant resistances

Resistance to water and heat loss from a plant community is an indication of how well the plants are adapted to withstand water deficit. The role of morphology and canopy structure in the water relations of a plant can be quantified by measuring the resistance offered by the plant to the transfer of water. This is especially important in xeric areas where water is often limiting to plant growth and development (Kramer 1969).

Methods and materials

Resistances to water vapor (R_w) and sensible heat fluxes (R_T) were determined for both vascular species using the hourly temperature readings from a thermister at 15 cm, relative humidity from a hygrothermograph (15 cm), leaf temperature from a thermocouple network, LE from lysimeter measurements, and H from equation 1.

Results and discussion

The resistance measurements, made in an attempt to quantify plant adaptation to water deficits (Table 6), are subject to criticism. The values only give an indication of how the plant responds to various environmental factors such as wind speed, radiation load, and relative humidity. The greatest source of error is probably that leaf temperature was measured on the raised beach and on the meadow roughly 100 m from the intensive study

Table 6. Vascular plant resistances (sec cm^{-1}) to water vapor and sensible heat transfers.

Plant species	Date	R_w		R_T
		$R_a + R_c$	R_l	
<i>Dryas integrifolia</i>	17 July, 1972	.29	20.08	.32
	18 July, 1972	.36	1.80	.40
	24 July, 1972	.47	4.88	.52
<i>Carex stans</i>	17 July, 1972	.26	15.74	.27
	18 July, 1972	.15	7.80	.16
	24 July, 1972	.63	15.71	.69

sites that recorded ambient conditions. The temperature (15 cm) at the stations was comparable to that recorded at the intensive study sites (within 2°C under stable conditions with a 4°C variation under fluctuating thermal regimes). Since H and LE are dependent upon temperature gradients between leaf and air, accurate temperature measurements (i.e. $\pm 0.5^\circ\text{C}$) are necessary to obtain reliable resistance values and hence the error.

The major resistance to water loss from *Dryas* is that offered by the leaf (R_l) and its tomentose lower epidermis (Table 6). The boundary layer (R_a) and canopy resistances (R_c) represented less than 10% of the total on two of the three days presented. The exception can be accounted for by a reduction in R_l rather than an increase in either R_a or R_c . This reduction in R_l is assumed to be as a result of surface wetting of the leaves.

Internal leaf resistances of *Dryas* varied greatly among the days presented (Table 6). On 17 July, there were fairly high winds and a high radiation load resulting in a water deficit with leaf water potentials of ca. -40 bars. Leaf resistance increased until 1300 hrs indicating gradual closure of stomata under moving air conditions (Bange 1953). The maximum resistance recorded on 17 July was 44 sec cm^{-1} and this was comparable with values for White Pine (*Pinus strobus*, 50 sec cm^{-1}) measured by Gates (1966). The resistance values for *Dryas* were also within the range of cuticular resistances for many tree species (37 to 380 sec cm^{-1}) presented by Holmgren et al. (1965). Stomatal closure is not the only factor that results in an increased leaf resistance. *Dryas* leaves curl at the edges as they dry and curling of leaves increases resistance substantially (Slatyer 1967).

The resistances during 24 July were different from those of either of the previous two days. These values represent the minimum resistance possible without surface wetting and were measured under conditions of low light, relative humidity, and moist soil conditions.

Leaf resistance of *Carex* indicates that water deficit at the meadow was relatively constant regardless of environmental conditions (Table 6). No difference between leaf resistances to water vapor transfer on 17 July and 24 July was observed even though the environmental conditions were very different. Since these leaf resistances were both consistent and high, the stomata must have been closed to a similar extent on the two days. This was a result of difficulty in replacing transpired water by absorption from cold and poorly aerated soil and led to low leaf water potentials. The maximum leaf resistance of *Carex* was 28 sec cm^{-1} and this value is much higher than the cuticular resistance of many crop plants (Kuiper 1961; Al-Ani and Bierhuizen 1971). Water on the outside of the leaves on 18 July reduced the measured leaf resistances as it did for *Dryas* but the reduction was less since *Carex* does not have a layer of hairs that can trap precipitation.

In general, both *Carex* and *Dryas* offer high resistances to water transfer from their tissue to the air. *Dryas* leaf resistances vary much more than those of *Carex* and the maximum observed for *Dryas* was twice that for *Carex*. The greater variation of *Dryas* leaf resistances indicates that this plant may be better adapted to withstand water deficit. *Dryas* has a higher resistance when the stomata are closed but it is able to transpire freely on days with moderate light loads and high soil moisture.

Ecological implications

The cushion growth form is predominant on the raised beach ridges. This growth form, exemplified by *Dryas integrifolia*, has a significant effect on how absorbed energy is dissipated from the plant. The cushion is tightly appressed to the ground surface and may be considered to lie within the earth's boundary layer. This results in an increased resistance to sensible and latent heat fluxes and causes high leaf temperatures and most of the incoming energy to be emitted as longwave radiation.

The crests of raised beaches are exposed to wind at all seasons which results in a shallow snow cover during the winter months (Courtin and Addison 1973). Courtin (1968) stated that abrasion by wind-borne ice particles in winter was a major cause of damage to krummholz in the alpine tundra and that the cushion growth form was well adapted to minimize this damage because of reduction of wind speed near the surface. This enables *Dryas* to colonize even the most exposed sites. In many such areas, the centre (higher) portion of the plant is dead, probably either as a result of abrasion of the most exposed parts during the winter or senescence of the oldest parts.

Dryas leaves decompose *in situ* producing an organic layer between live leaves and the surface of the soil. A similar observation was made by Heilborn (1925) for a number of cushion plants of the Ecuadorian Paramos and Courtin (1968) for *Diapensia lapponica* on Mt. Washington, New Hampshire. It appears, therefore, that this may be a relatively common characteristic of the cushion growth form. Although this layer of organic material is probably more important for plant growth in the nutrient budget than in the energy budget of the plant, it significantly reduces the soil heat flux beneath the plant. The insulative properties are sufficiently good to isolate the plant leaves from the soil with respect to temperature.

Dryas leaves are adapted to the extreme environmental conditions to which they are exposed. The cuticle reduces latent heat flux by minimizing cuticular transpiration from the upper surface. The densely tomentose lower epidermis reduces sensible heat flux from the abaxial surface. Thus two major methods of energy dissipation are largely restricted to only one leaf surface and the efficiency of energy transfer is reduced substantially. High *Dryas* leaf temperatures (i.e. 45°C) seen on 17 July as a result of the inability of the plant to dissipate energy. High leaf temperatures increase respiration much more than they do photosynthesis and result in a decrease in net photosynthesis (Mayo et al. this volume). Frequent incidence of cloud in the Arctic reduces radiation load on the surface (Thompson 1967) and hence high *Dryas* leaf temperatures are rare. Leaf temperatures reflected the radiation load and were normally 5° to 15°C above ambient air temperature during the high sun hours (0600 to 1800 hr). Since tissue temperatures were usually above those of ambient air, plant physiological processes were more active when air temperatures indicated that the process should be temperature limited. The probable advantage of this is to give the plant a

longer period of adequate growing conditions, an important consideration in a site where plants must withstand severe drought over much of the snow-free period. An increase in latent heat flux has been shown from rain-wetted *Dryas* leaves. Evaporation of this water tends to keep leaf temperature low and it is especially important if a day of high incoming radiation follows precipitation.

The presence of lichens on the beach ridge appears to have a significant effect on the water relations of the site. Fruticose lichens had a higher evaporation rate than did adjacent bare soil. Because both coarse bare soil and lichens had a net gain of water over the summer and because there was little or no vascular plant cover in the areas dominated by these lichens, the impact of fruticose lichens on the vascular plants was minimal. The crustose lichens, on the other hand, were closely associated with vascular plants and were effective in conserving water as compared with adjacent bare soil. These lichens, therefore, improved the soil water relations of the site, a definite advantage to both vascular and non-vascular plants in an area where water appears to be limiting.

The meadow was not, in general, a water limited system. Vascular plants must absorb water through their roots, but both cold soil and low oxygen tensions at this site reduce membrane permeability and, therefore, water uptake. As a result *Carex* plants occasionally showed stress conditions similar to those of *Dryas* on the raised beach (ca. -40 bars). Soil factors appeared to impede water uptake sufficiently to cause stomatal closure with only a limited evaporative demand. The characteristic "midday stomatal closure" frequently observed in temperate species under water deficit appears to be expanded to a 12 hr period (ca. 0700 to 1800 hr). It was also noted that there was little variation in the leaf resistance of *Carex* during the day, indicating that fluctuations in stomatal aperture were minimal. Although the incident energy received by *Carex* was similar to that of *Dryas*, net radiation was higher because of lower reflectance of shortwave radiation and cooler leaf temperatures resulting in a lower reradiation term. Leaf temperature in itself is a reflection of the energy dissipating capabilities of a plant or plant community. *Carex*, because of its upright growth form, sparse canopy and large effective surface area, was able to dissipate energy much more easily than *Dryas* and, therefore, leaf temperature was lower. A comparison of canopy and boundary layer resistance of the two plants showed that when the wind speed was the same (17 July at the beach ridge and 18 July at the meadow), the resistance to energy dissipation offered by *Dryas* was twice that by *Carex*.

Both physical (boundary layer + canopy) and physiological (leaf) resistances to water vapor and sensible heat transfers are higher in *Dryas* than they are in *Carex*. High resistance to water vapor transfer implies a high resistance to CO₂ entry which, in turn, implies a lower photosynthetic rate. The maximum rate of carbon assimilation by *Dryas* was 4.2 mg CO₂ g⁻¹ hr⁻¹ as compared with 13 mg CO₂ g⁻¹ hr⁻¹ by *Carex* (Mayo et al. this volume). A similar pattern was observed when *Diapensia lapponica* was compared with *Carex biglowii* (Hadley and Bliss 1964, Courtin 1968) in an alpine environment. Low photosynthetic rates of *Dryas* were overcome to a large extent by positive net assimilation rates throughout the 24 hr arctic day except under high light loads when leaf temperatures were high (20°C) (Mayo et al. this volume).

The canopy of the *Carex* microsite (*Carex stans* with an understory of moss) had a marked effect on the soil energy flux. Because of the two-layered structure on the plant community, most of the incident radiation was

intercepted before it reached the ground. Also, with over 50% of R_n dissipated as LE, surface temperatures were low and there was a shallow gradient between the surface and the permafrost below. This resulted in a reduction of over 50% in the soil heat flux compared with an area devoid of vegetation (i.e. a shallow pool). A self-perpetuating system was thus produced, with the plant community preventing the frost table from thawing, the frost table reducing drainage, and the resulting waterlogged conditions encouraging the establishment of a *Carex*-moss community.

Carex stans, although it does not appear to be well adapted to saturated soils, is able to survive and function under these conditions. Since most vascular species are not able to withstand poorly aerated soil, competition for nutrients, light, and space is much reduced with the exclusion of many species from these areas. This results in a distinct ecological advantage for this species in waterlogged soils. Waterlogging is also of advantage to many moss species as they do not have a root system to replenish the water lost through evaporation. Since the bases of the moss stems are in water at the meadow, water movement to the aerial parts is possible by capillary action on the outside of the stem. This ensures that water is plentiful in the growing tissue at the apex of the shoot.

In general, the raised beach presents a much more hostile environment for plant growth than does the meadow. *Dryas integrifolia* at the beach ridge appears to be well adapted to withstand water deficit and to trap incoming radiation, whereas *Carex stans* at the meadow does not seem to have either of these adaptations. *Carex* is, however, able to withstand cold and poorly aerated soil conditions that characterize the highly organic meadow sites on Devon Island.

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