Adaptations of *Luzula confusa*
to the Polar Semi-Desert Environment

P.A. ADDISON[1] and L.C. BLISS[2]

ABSTRACT. *Luzula confusa* is both morphologically and physiologically adapted to the polar semi-desert environment of the western Queen Elizabeth Islands. This species combines the more efficient graminoid photosynthetic system and a less drought-resistant mechanism with some of the cushion plant energy-trapping characteristics such as tufted growth form and persistence of dead leaves, with consequent thicker boundary layer. In this manner, the plant is able to assimilate carbon throughout the 24-h arctic day. The species utilizes the most favorable part of the growing season by rapid initiation of growth via relatively high photosynthetic rates, especially at low temperatures. This species is very responsive (net assimilation rates) to small changes in leaf temperature and leaf water potential. This permits the species to take advantage of small rises in leaf temperature (leaves normally 5 to 8°C) and to adjust to high VPD and low leaf water potential during the occasional drought.

The slow-growing, long-living conservative strategy of this species appears ideally suited to areas that are limited in their vascular plant cover because of rigorous environments. Within the range of habitats available, *Luzula confusa* predominates in sites of intermediate moisture with abundant cryptogams. It does not occur in the polar deserts with their drier surface soils except in snowflush communities.

Key words: *Luzula confusa*, High Arctic, plant/water relations, net photosynthesis, plant phenology, polar semi-deserts

RÉSUMÉ. La *Luzula confusa* est adaptée de façon morphologique et physiologique au milieu polaire semi-désertique dans l'ouest des îles Reine-Élizabeth. Cette espèce combine un système très efficace de photosynthèse de graminé et un mécanisme à résistance moins élevée à la sécheresse avec certaines des caractéristiques tampons retenant l'énergie de la plante telles que la forme en touffe, la persistance des feuilles mortes et la couche limite plus épaisse qui en résulte. De cette façon, cette plante peut assimiler le carbone tout au long des 24 heures du jour arctique. Pendant la partie la plus favorable de la saison de croissance, l'espèce croît par initiation rapide grâce à son taux de photosynthèse relativement élevé, et surtout grâce aux basses températures. Cette espèce réagit de façon marquée (taux d'assimilation nette) aux changements minimes de température des feuilles et à la teneur d'eau maximale des feuilles, ce qui permet de profiter des hausses minimes dans la température des feuilles (température normale de 5° à 8°C) et de s'adapter à un VPD élevé et à la teneur d'eau peu élevée des feuilles au cours de sécheresses occasionnelles.

La stratégie conservatrice de croissance lente et de longue vie de cette espèce semble être parfaitement convenable aux régions qui comportent une végétation vasculaire limitée à cause du milieu rigoreux. Parmi les différents habitats possibles, la *Luzula confusa* prédomine dans les sites à humidité moyenne contenant d'abondants cryptogames. Elle ne croît pas dans les déserts polaires à sols de surface plus secs, sauf dans les communautés à taches de neige.

Mots clés: *Luzula confusa*, nord de l'Arctique, relations plantes-eau, photosynthèse nette, phénologie des plantes, semi-déserts polaires

INTRODUCTION

Abiotic rather than biotic factors are central in controlling plant growth and reproduction in the Arctic (Bliss, 1971; Billings, 1974). In the High Arctic, where environmental conditions are severe (Courtin and Labine, 1977; Addison and Bliss, 1980), there are few plant life forms adapted to survive a 40-50 day growing season where average daily air temperatures at plant height (1-5 cm) are seldom above 3 to 6°C. The life forms that predominate are cushion, rosette, and tufted graminoid.

Graminoids other than sedges are dominant components of many upland plant communities in the Western Queen Elizabeth Islands (Bird, 1975; Bliss and Svoboda, 1984). *Luzula confusa* and *L. nivalis* are common in moist habitats. Both are widely distributed circumpolar species that are found on soils ranging from clay loams to sands.

A detailed study of plant growth and ecophysiology of *Luzula confusa* was undertaken because the species is so common on these northern islands (Porsild, 1964) and because its tufted graminoid growth form is representative of other species. The study was conducted on King Christian Island, because this species predominates there in many plant communities, and because an existing camp facilitated the research.

King Christian Island (ca. 1100 km² in area) has a low domal profile with long, low scarps and gentle slopes. Most of the island consists of alternating beds of sandstones, mudstones, and shales from Isachsen and Christopher Formations of Lower Cretaceous age (Balkwill and Hopkins, 1978). Water erosion plays a dominant role in the dendritic drainage patterns that characterize the low relief. Microtopographic features in the form of soil hummocks (10-20 cm in diameter), soil polygons, and soil stripes (50-150 cm across) are common, the product of needle ice, desiccation cracks, and soil erosion.

Summer climate is characterized by low average temperature (2.2-2.9°C), low total precipitation (50-65 mm), moderate average wind speed (3.3 m·s⁻¹), and high incidence of cloud and fog (78-87%) (Addison and Bliss, 1980). Although mean temperature varies little from year to year, the summer season is variable owing to differences in cyclonic activity and time of snowmelt. Atmospheric humidity is high whereas radiant heat load and ambient temperatures are low. This results in an energy balance that is dominated by atmospheric rather than by surface conditions, where diffuse rather than solar radiation predominates.

On King Christian Island, as elsewhere in these northern islands, plant cover is generally controlled by substrate condi-

[1]Canadian Forestry Service, Northern Forest Research Centre, Edmonton, Alberta, Canada T6H 3S5
[2]Department of Botany, University of Washington, Seattle, Washington 99195, U.S.A.

tions. The greatest plant cover occurs in a band 1.5-2.0 km wide and about 1 km from the coast on fine-textured soils of recent marine origin. Inland valleys also have considerable plant cover, part of the polar semi-desert landscape, with vascular plants providing 10-20% cover and cryptogams 40-70% cover (Bliss and Svoboda, 1984). Elsewhere on ridges and on the coarse-texture substrates derived from the Isachsen Formation, total plant cover averages only 1-3%. This is representative of the barren polar deserts (Bliss et al., 1984).

This study was conducted within a cryptogam-herb plant community dominated by *Luzula confusa*, *L. nivalis*, *Alopecurus alpinus*, and *Papaver radicatum* (Bliss and Svoboda, 1984). The objectives were to determine the morphological and physiological adaptations of *Luzula confusa* that enhance growth and survival in the polar semi-desert environments exemplified by King Christian Island.

METHODS AND MATERIALS

Plant Characteristics

Ten plants, approximately 15 cm in diameter, were collected to estimate number of leaves produced per year, average age of tillers, plant age, and structure of above-ground and below-ground components. The time required for initiation of growth in the spring was determined by measuring the average green leaf length of 60 plants and the average depth of the active layer during snowmelt.

Five cores of *L. confusa* (28 cm² × 15 cm deep) were taken at the peak of the growing season (July) to determine standing crop in the above-ground live and dead rhizome and root components. Cores were divided into sections at depths of +2, 0, −1, −5, −10, and −15 cm. Most divisions were based on plant characteristics; +2 cm represented the top of the moss layer; 0 cm, moss-mineral soil interface; and −1 cm, maximum penetration of rhizomes. The divisions at −5, −10, and −15 cm were arbitrary and coincided with the positions where soil moisture and temperature were measured. No attempt was made to distinguish between live and dead roots.

Water Relations

Leaf water potential (Ψ_ℓ) was determined with chamber psychrometers constructed after the design of Mayo (1974). The psychrometers were placed in a water bath to control temperature and to prevent the establishment of thermal gradients in the psychrometer body. Water potential was measured after a 2-h equilibration time that was predetermined experimentally. Psychrometers were calibrated monthly with KCl solutions of known osmotic potentials. In all cases, the tillers used for water potential measurements were collected from the center of the plant. The water potential of a central tiller was within the range given by the 95% confidence limit of the mean four measurements taken around the perimeter of the clump six times throughout a given day.

Osmotic plus matric potential ($\Psi_\pi + \Psi_\tau$) was determined with chamber psychrometers after freezing the tissue to break the cell membranes and reduce turgor to zero. In the field,

liquid propane ($-42\,°C$) was used to freeze the tissue, whereas in the laboratory liquid nitrogen ($-196\,°C$) was used. Turgor potential (Ψ_ρ) was calculated by subtracting $\Psi_\pi + \Psi_\tau$ from Ψ_ℓ.

Atmospheric humidity was measured with a hygrothermograph (10-25 cm), and water loss from entire plants was determined by weighing sod blocks (Addison and Bliss, 1980). Leaves from the sod blocks were harvested and leaf area was determined using a linear regression of area *vs.* oven dry weight (leaf area (cm²) = $-4.1 + 390 \times$ oven dry weight (g); $r^2 = 0.79$). Leaf area for the regression was determined by the Ballotini glass bead technique (Thompson and Leyton, 1971).

All plants used in laboratory experiments were collected in the field at the end of the growing season, potted in their native soil, and given a "dormancy" period of more than two months at $-5\,°C$. The plants were then grown under a constant diurnal pattern of light and temperature in a growth chamber (Model M15, Environmental Growth Chambers). Air temperature ranged from $0\,°C$ (night) to $10\,°C$ (day), and light from 0.13 $J\cdot cm^{-2}\cdot min^{-1}$ to 1.00 $J\cdot cm^{-2}\cdot min^{-1}$ (photosynthetic photon flux density of 0 to 540 $\mu mol\cdot m^{-2}\cdot s^{-1}$.

The resistance that *L. confusa* leaves imposed on water flux was calculated for periods when the plant showed signs of water deficit (i.e. $\Psi_\rho < 0.1$ MPa) in order to estimate the capability of the plant to withstand drought. The total resistance of the water transfer pathway from leaf to air (R_w) was calculated from Equation 1 and the resistance owing to the laminar boundary layer of the leaves and the canopy was calculated and subtracted from the total:

$$R_w = \frac{273}{PT} \rho \frac{e_s - e_a}{E} \qquad (1)$$

where P is atmospheric pressure; T is air temperature ($°K$); ρ is density of water vapor ($g\cdot cm^{-3}$); E is water loss ($g\cdot cm^{-2}\cdot s^{-1}$); and e_s and e_a are the vapor pressure of water within the leaf and in the air respectively. Systematic errors in the calculation of the resistance to water flux are in the order of 1.4 $s\cdot cm^{-1}$ primarily owing to inaccuracies in both hygrothermograph and sod block measurements.

The sum of boundary layer and canopy resistances was calculated by combining the heat transfer equation of Raschke (1960) and the ratio of the diffusivities of water vapor and heat in air (Slatyer, 1967) into Equation 2:

$$r_a = \frac{1.54\, c \rho (T_\ell - T_a)}{H} \qquad (2)$$

where r_a is the resistance of the boundary layer and canopy to water-vapor transfer ($s\cdot cm^{-1}$); c is specific heat of air ($J\cdot g^{-1}\cdot °C^{-1}$); ρ is density of air ($g\cdot cm^{-3}$); T_ℓ and T_a are temperature ($°C$) of leaf and air, respectively; and H is sensible heat flux ($J\cdot cm^{-2}\cdot s^{-1}$) calculated from the energy budget (Addison and Bliss, 1980). The assumption that sensible heat flux was equal from both leaf surfaces whereas water loss was from only the abaxial surface was incorporated into Equation 2.

Leaf resistance was calculated by subtracting r_a from r_w. Because of the method used, the possible relative error in r_a is

extremely large but since r_a was typically small, the errors are not critical to leaf resistance calculations. If the resistance of the intercellular spaces, mesophyll, and cuticle were nearly constant as they usually are, it follows that changes in leaf resistance were caused by changes in stomatal aperture.

The response of *L. confusa* to decreasing water content was described in the laboratory at two phenological stages (before flowering and during senescence). Plants were well watered and enclosed in plastic bags for 24 h in order to maximize both Ψ_ℓ and relative water content (RWC). All tillers of a plant were assumed to have the same RWC and Ψ_ℓ after this treatment. Water balance of a plant was estimated by measuring RWC of four entire, non-flowering tillers. These tillers were weighed, floated on distilled water for 4 h, blotted dry, and re-weighed before they were dried at 80 °C for 24 h. Other tillers from the same plant were detached, weighed, and allowed to lose known amounts of water to provide a range in RWC, Ψ_ℓ, $\Psi_\pi + \Psi_\tau$, and Ψ_ρ before being transferred to chamber psychrometers. Water potential, its components, and oven dry weight were determined as already described. Relative water content was defined as the percent water present based upon the water content after the tillers had been floated on water and blotted dry. The average RWC obtained after enclosing the plant for 24 h in a plastic bag was >95% in all cases.

Net CO_2 Assimilation

In both the field and the laboratory net assimilation rate (NAR) was used as an indication of plant metabolism in order to evaluate the influence of extrinsic (environmental) and intrinsic (genetic) factors on plant growth and survival. Net assimilation was determined for individual tillers that were enclosed in cylindrical cuvettes 5 cm long and 1.5 cm in diameter. Two cuvettes were used in an open cuvette-gas analysis system (Šesták *et al.*, 1971) on a time-shared basis. Carbon dioxide flux from air to plant was determined by measuring the difference in CO_2 concentration between a sample and a reference air stream with a Beckman Model 865 Infra-red Gas Analyser (IRGA). Calibration was carried out every 8 h with known CO_2 concentration in air. At the end of the measurement period, enclosed tillers were harvested, dried at 80 °C for 24 h, and weighed. Conversion to leaf area was accomplished as described above.

In the field, the IRGA system was housed in a heated tent and insulated with plastic foam to maintain optimum operating temperatures. The power supply was a 2500 W gas-powered generator, and both voltage and frequency were kept constant (110 VAC @ 60 Hz) by varying a "dummy" load of two 250 W light bulbs. The generator was kept downwind of the air intake for the air flow system in all times.

In the laboratory the plants were grown under conditions described under *Water Relations*, but for experimental purposes they were transferred to a second growth chamber. Air for the flow system was supplied from the central air conditioning system of the building, and two 10-litre mixing bottles were used to stabilize CO_2 levels in ambient air. In both laboratory and field studies it was impossible either to control

or to measure atmospheric humidity in the cuvette with the instrumentation available.

Photosynthetic Photon flux density (PPFD) was measured with a Lambda quantum sensor and measurements of both global and total incoming radiation were made according to methods described by Addison and Bliss (1980).

Leaf and air temperatures, both inside and outside of the cuvette, were measured with thermocouples (0.13 mm in diameter) and were monitored with a Honeywell Multipoint Recorder. Leaf thermocouples were in contact with the abaxial leaf surface. Temperatures within the cuvette were kept within 5 °C under sunny conditions and within 2 °C on overcast days by adjusting the flow rates between 50 and 150 ml·min^{-1} through the cuvette.

Soil moisture was measured gravimetrically every 2 h. Leaf water potential of *L. confusa* tillers adjacent to the cuvettes was determined hourly as previously described.

Light and Temperature Response

Pairs of *L. confusa* plants, each with one tiller enclosed in a cuvette, were given a 2-h period under each condition of PPFD and temperature. Temperatures were set from 0-25 °C in 5 °C intervals. Light from cool white fluorescent tubes supplemented by incandescent bulbs was given at 0, 150, 350, 550, 900 and 1300 μmol·m^{-2}·s^{-1} PPFD. For the two highest photon flux densities, growth chamber lights were supplemented by a 1000 W Tungsten-filament bulb with water jacket. Readings of gas exchange were taken during the last 0.5 h of the 2-h period and a maximum of eight replicates was used for every combination of temperature and photon flux density.

Soil Drying Response

Four plants were grown under a controlled environment for 20 days (d) and watered every 3 d. For the following 15 d, they received constant temperature conditions (10 °C) but with varying photon flux density (0 to 550 μmol·m^{-2}·s^{-1}). During that time watering was stopped, but relative humidity in the chamber was maintained at about 60%. The net assimilation rate (NAR) of one tiller from each plant was measured daily at approximately noon throughout the drying period. The tiller was enclosed in the cuvette only for the 1-h period required to measure NAR. The water potential of the plant was determined concurrently with NAR by harvesting and measuring another tiller from the same plant. It was assumed that all tillers of one plant had the same NAR and water potential.

Effect of Phenology

Net assimilation rates of various non-flowering tillers from a single *L. confusa* plant were measured continuously for a 24-h period under growth chamber conditions at selected times during the growing period. The times represented four plant phenological stages (pre-flowering, anthesis, post-flowering, and dieback).

TABLE 1. Standing crop components of *Luzula confusa* on 21 July 1974 (mean ± 95% confidence limits). Area is based on the cover of *L. confusa* in the cryptogam-herb community (8%).

Component	Standing Crop (g·m⁻²)	(%)
Above-ground		
Live	1.0 ± 0.8	3
Dead	15.8 ± 9.0	55
Below-ground		
Rhizomes	5.5 ± 3.0	19
Roots	6.4 ± 2.1	22
Total	28.7	99

RESULTS AND DISCUSSION

Growth Form

The *L. confusa* plants of the cryptogam-herb community were large compared with most plants on King Christian Island. The plants were about 20 cm in diameter and approximately 4 cm high. Moss (mainly *Ditrichum flexicaule*) grew between the tillers, forming a mat about 2 cm thick. Only 6% of the above-ground standing crop of *L. confusa* was live (Table 1), and hence it was standing dead material that gave the plants their characteristic appearance. Total below-ground (including rhizomes) to above-ground biomass ratio was 0.29:1, similar to the 0.21:1 measured by Bell and Bliss (1978) on plants nearby. Most roots (73%) were in the top 5 cm of the mineral soil (Table 2) in spite of a 45 cm deep active layer in August. Observations by Bell and Bliss (1978) indicate that rooting of most species on King Christian Island is confined to the upper half of the active layer.

TABLE 2. Vertical distribution of living and dead roots of *Luzula confusa* on King Christian Island (mean ± 95% confidence limits). Area is based on the cover of *L. confusa* in the cryptogam-herb community (8%).

Depth (cm)	Standing Crop (g·m⁻²)	(%)
Moss (+2-0)	0.4 ± 0.3	7
0 - −1	1.8 ± 0.6	28
−1 - −5	3.0 ± 1.6	45
−5 - −10	1.0 ± 0.7	16
−10 - −15	0.3 ± 0.3	4
Total	6.4 ± 2.1	100

Since both above-ground and below-ground parts of *L. confusa* were concentrated near the soil surface, the growth form appears to be ideally suited to utilizing the warmest microenvironment. Persistence of dead material in its upright position decreased the influence of wind on heat and water-vapor flux and helped to raise leaf temperature above those of ambient air. Leaf temperatures were normally 1-2 °C higher than ambient air temperature and on sunny, windless days were 5 °C higher.

The large amount of standing dead material (94% of above-ground standing crop) also appears to aid in winter protection of living plant parts. Observations during August snowstorms showed that snow accumulates around the dead material; this would protect the basal meristem and winter-green portions of the leaves from both abrasion by wind-borne ice particles and temperature extremes. Spring snow depth averages 10-15 cm in habitats where *L. confusa* predominates. In the spring, trapped snow melts and provides a supplementary water supply to the plant via roots in the moss layer.

Standing dead material remains intact for a long period of time (> 20 yr, as estimated below) because grazing by animals is negligible and the upright growth form puts the leaves in an unfavorable environment for decomposition. S. Visser (University of Calgary, pers. comm. 1976) found that both fungal biomass and number of fungal species colonizing dead *L. confusa* leaves from this site were extremely low compared with fungal populations on leaves in more temperate regions. Winter-green leaf bases characterize this species as well as most other species on this island and elsewhere in the High Arctic (Bell and Bliss, 1977).

Age

Individual tillers produced 14.5 ± 1.3 (mean ± 95% confidence limits) leaves during their lives. Each tiller had four leaves present during the growing season, two produced each year; leaves live for two years. This estimate is identical to that of Bell and Bliss (1978) on King Christian Island and that of Sørenson (1941) on Greenland. With two leaves produced yearly, the average life span of a tiller is 7 yr, similar to age estimates for *L. confusa* tillers on Greenland (Sørenson, 1941).

Plant age was estimated by multiplying the number of tillers along the longest rhizome branch by the replacement time. Since two tillers were alive at all times on each rhizome branch and since the life expectancy of a tiller was ≃ 7 yr, replacement time was 3.5 yr. The average number of tillers in a row was 32.2 ± 5.6, and therefore plants had an estimated age of 90 - 130 yr. Since it was not possible to trace the rhizome to the very first tiller produced, these age estimates are minimum values.

Reproduction

Sexual reproduction appeared to be ineffectual, and in fact, no viable seed was produced during three years of study (Bell and Bliss, 1980a). Reproduction was asexual through tillering from underground rhizomes. Each tiller died after flowering, although not all tillers flowered. Flowering appeared to stimulate rhizome branching, possibly through the loss of apical dominance as a result of the shift from leaf to floral meristem. Since no viable seed was found, even flowering appeared to be more important for asexual than for sexual reproduction. It is hypothesized that two exceptionally warm and long summer seasons are required for the production of viable seed: the first to initiate floral primorida, and the second to permit seed maturation. Since seedling establishment of nearly all vascular

species is infrequent in the High Arctic (Bell and Bliss, 1980a; Sohlberg and Bliss, 1984), it appears that an exceptionally warm year must be followed by a warm moist year to permit seedling establishment. The higher-than-normal temperatures are needed to promote seed germination and higher-than-normal surface soil moisture is essential for seedling establishment (Bell and Bliss, 1980a). Judging from the even age of the *L. confusa* within the cryptogam-herb community studied, this sequence is very rare and may have a return interval of about 100 yr. Seedling survival, however, is enhanced by a moss substrate since it provides a higher and more consistent moisture supply, higher surface temperature and reduced wind velocity (Addison and Bliss, 1980; Sohlberg and Bliss, 1984), and less resistance to root penetration than does mineral soil (Bell and Bliss, 1978).

Growth

Measurements of active layer depth and green leaf length in spring indicated that leaf expansion commenced when the active layer was <6 cm, and this amount soil thaw occurred in <2 d. This compares favorably with observations of arctic graminoids at Barrow, Alaska (Tieszen, 1972), at the southern edge of the High Arctic.

L. confusa has a periodic growth pattern (Sørenson, 1941), and on King Christian Island, leaves started to senesce 45-50 d after the initiation of growth. Root growth also dropped to almost zero 49 d after snowmelt (Bell and Bliss, 1978). A similar growing period (55 d) was observed under controlled environmental conditions where photoperiod, photon flux density, diurnal temperature oscillation, and soil moisture remained constant. The periodicity was apparently unchanged by flowering, and the mechanism controlling it is unknown. It is thought that autonomous interruptions in growth may only be of short duration under favorable conditions (Sørenson, 1941). In exceptionally long, warm seasons the plant may still be able to produce viable seed, but this aspect was not examined within controlled environment conditions.

Water Relations

Leaf water potential (Fig. 1) was low (< -1.0 MPa) in early July 1974 but increased over a 10-d period to about -0.5 MPa where it remained for most of the growing season. This trend did not appear to result from the soil moisture regime, since soil water potential of the top 5 cm was above field capacity (-0.03 MPa) for the entire summer season (Fig. 2). The low spring values (Fig. 1) appeared to result from low soil temperatures (1-2°C) that reduced root water uptake, rather than from dry air that increased water flux from leaves. The seasonal pattern of leaf osmotic plus matric potential (Fig. 1) followed that of Ψ_ℓ, and turgor potential remained fairly constant at $\cong 0.6$ MPa.
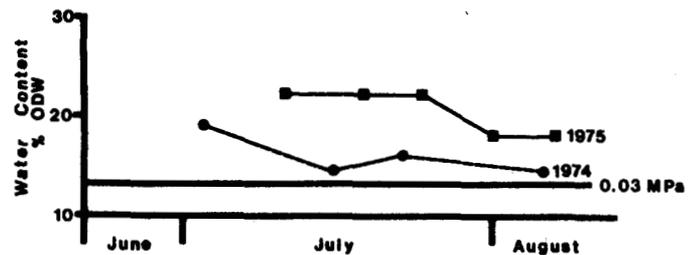
FIG. 2. Soil moisture (0-5 cm) in % of oven dry weight (ODW) of the cryptogam-herb community during the summers of 1974 and 1975. Values are averages of four measurements and dashed line represents the water content at -0.03 MPa.

Vapor pressure deficit varied little throughout the season and the mean value (<0.05 kPa) was less than is considered typical of either arctic (0.6-0.8 kPa; Lewis and Callaghan, 1974) or alpine (0.8-1.0 kPa; Bell and Bliss, 1980b) environments.

In the laboratory, when plants were watered every 3 d, Ψ_ℓ was $\cong -0.4$ MPa for most of the growing period (Fig. 3). The lower Ψ_ℓ and ($\Psi_\pi + \Psi_\tau$) values recorded in spring in the field (Fig. 1) did not occur in the laboratory. This indicates that field environmental conditions are responsible for the depressed field values, rather than characteristics of the plants during elongation.

L. confusa exhibited severe water deficit (i.e. $\Psi_\rho < 0.1$ MPa) on only one occasion (27 July 1974) during the three

FIG. 1. Leaf water potential (Ψ_ℓ) and osmotic plus matric potential ($\Psi_\pi + \Psi_\tau$) of *Luzula confusa* during the summer of 1974.
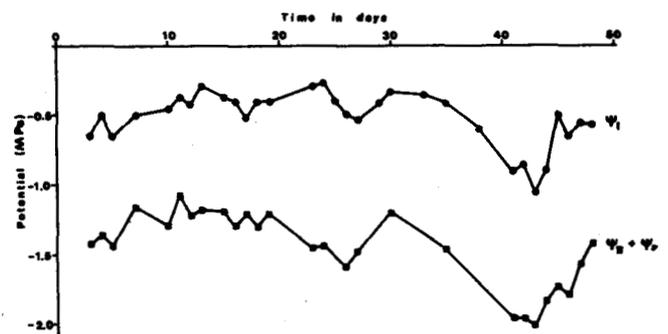
FIG. 3. Leaf water potential (Ψ_ℓ) and osmotic plus matric potential ($\Psi_\pi + \Psi_\tau$) of *Luzula confusa* during a growing period in the laboratory. Values are averages of four readings taken between 0800 and 1000 h.

years of field study. Incoming radiation on this day reached the highest value recorded $(4.81 \, \text{J} \cdot \text{cm}^{-2} \cdot \text{min}^{-1})$ and the five previous days had had no precipitation or fog. In the early morning (0400 h) transpiration started to increase (Fig. 4c) but at 0800 h there was a rate reduction. This decrease in transpiration could not be related to leaf temperature, air humidity, or the radiant heat load. It appears that transpiration exceeded water uptake by the roots, resulting in increased leaf water deficit and stomatal closure. Water and turgor potentials (Figs. 4a and 4b, respectively,) were both low at the same time. Leaf resistance (Fig. 4d) increased substantially, presumably owing to lower Ψ_ℓ and Ψ_ρ. The drop in turgor, Ψ_ℓ, and transpiration appears to stem from the inability of the plant to draw water from cold soils. Soil temperature $(-5 \, \text{cm})$ at 0800 hr was only 4°C but had increased to 10°C by 1200 h. A second

reduction in leaf water potential, turgor, and transpiration, accompanied by an increase in leaf resistance, occurred at 1200 h. Vapor pressure gradient from leaf to atmosphere increased from 0.30 kPa at 0800 h to 0.64 kPa at 1200 h. The second reduction in transpiration appears to be the "midday depression" of transpiration reported by Gates (1965) and others for mesophytic plants. The final reduction in transpiration at 2000 h can be explained by the reduction in leaf temperature to that of the ambient air, resulting in a reduction in vapor pressure deficit.

On most days during the summers of 1973 - 1975, water and turgor potentials were consistent and high (-0.35 and 0.8
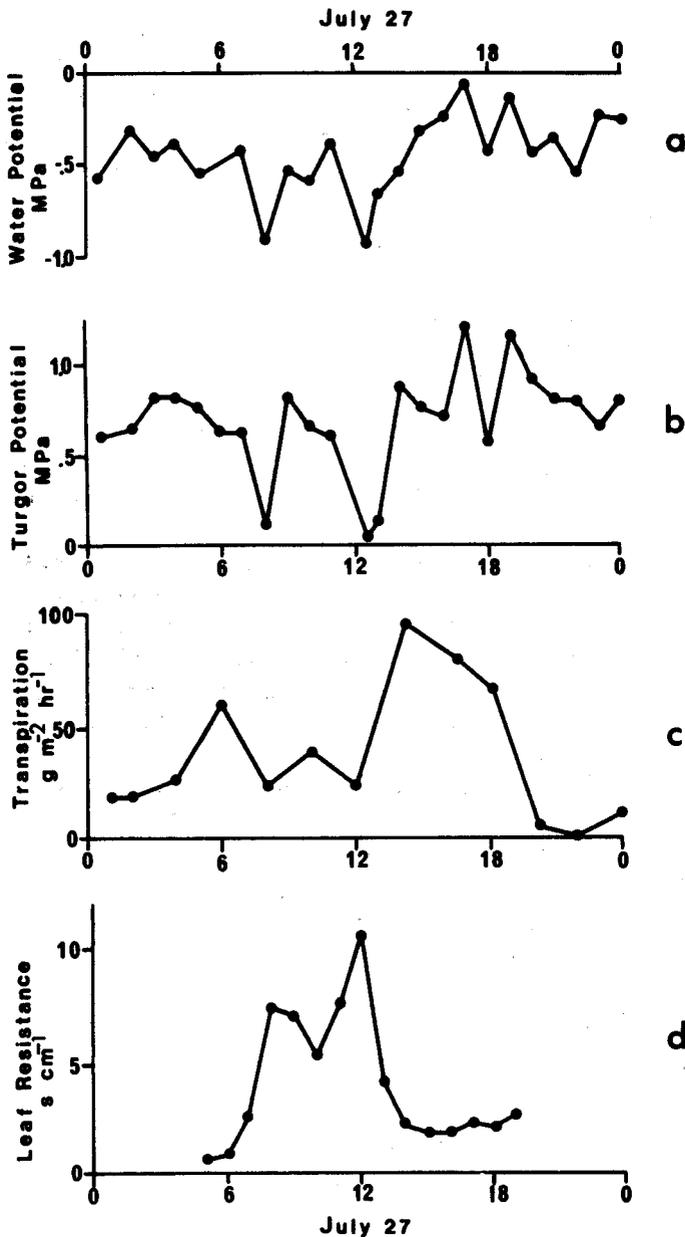
FIG. 4. Leaf water potential (a), turgor potential (b), transpiration (leaf area basic) (c), and leaf resistance to water flux (d) of *Luzula confusa* during 27 July 1974.
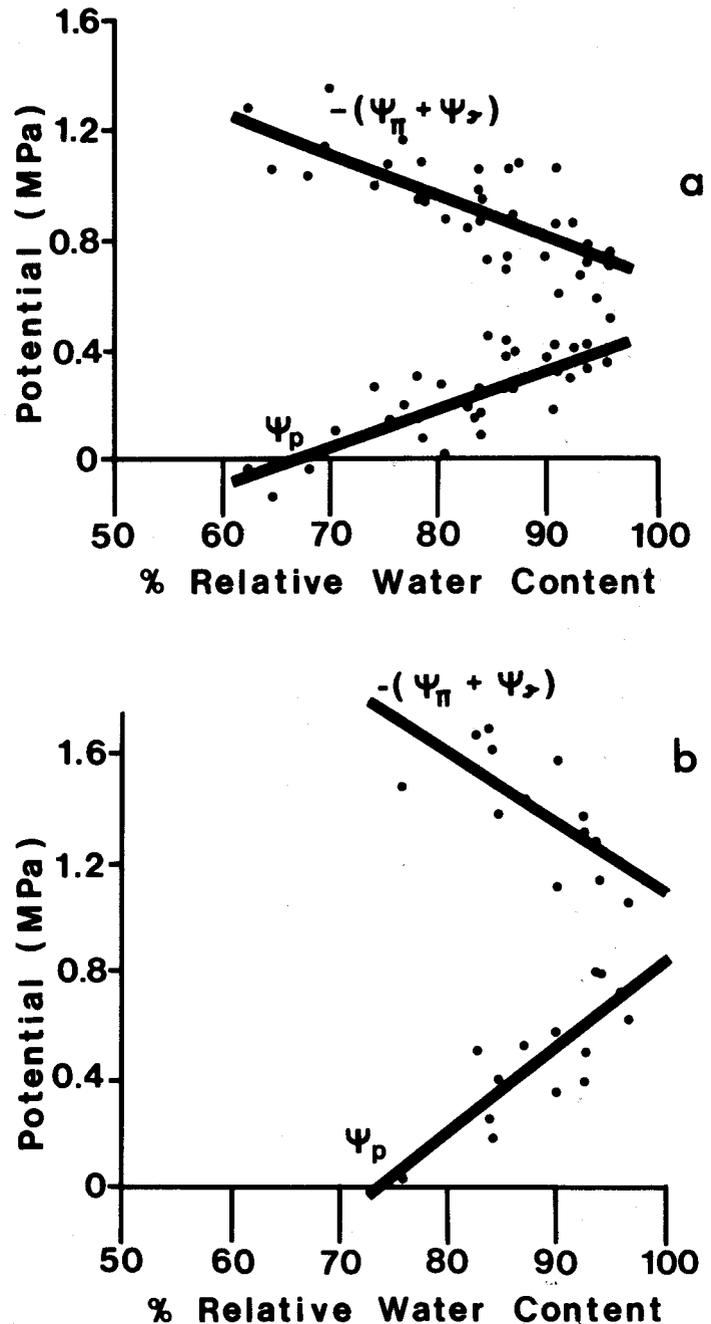
FIG. 5. Linear regressions of osmotic plus matric potential ($\Psi_\pi + \Psi_\tau$) and turgor potential (Ψ_ρ) vs. relative water content of *Luzula confusa* before (a) and after (b) flowering.

MPa, respectively) and transpiration was low. On such days, leaf resistance was normally less than 2 s·cm^{-1} throughout the day. The minimum leaf resistance of *L. confusa*, (0.5-1.0 s·cm^{-1}), calculated from the energy budget components, was comparable with that of plants growing in moist environments in both alpine (0.6-1.4 s·cm^{-1}; Ehleringer and Miller, 1975) and arctic (1-3 s·cm^{-1}; Stoner and Miller, 1975) environments.

Laboratory studies on the response of *L. confusa* to water deficit showed a shift with phenological stage (Fig. 5). There was a significantly greater reduction in turgor with decreasing relative water content in plants at the end of the growing season (Fig. 5b) than those at the beginning (Fig. 5a) (F_s test of regression lines, $p < 0.05$). This differential in cell wall elasticity appears to be a mechanism that allows the plant to survive late-season droughts and maintain sufficient water in its tissue to allow translocation of materials out of the leaf as it begins senescence. There was also a significantly greater reduction in $\Psi_\pi + \Psi_\tau$ with decreasing relative water content at the end vs. the beginning of the growing season. This is perhaps a response to senescence (greater solute concentration) and an increase in tissue cold hardiness.

Net CO$_2$ Assimilation

Temperature appeared to have the greatest effect of any environmental factor on net assimilation rate (NAR). Using 60 h of field NAR measurements at the height of the growing season (23-26 July 1975), a significant amount of the variability in NAR was accounted for by the regression of NAR on log temperature above a threshold of 3°C (NAR [mg CO$_2$·g^{-1}·h^{-1}] = −9.104 + 21.015 [log$_{10}$ °C]; $p < 0.001$). Below 3°C, photon flux density accounted for a significant amount of the variability in NAR (NAR [mg CO$_2$·g^{-1}·h^{-1}] = −1.018 + 0.012 PPFD; [µmol·m^{-2}·s^{-1}]; $p < 0.001$). Since leaf temperature was normally above the 3°C threshold, CO$_2$ uptake was more strongly coupled to temperature than to light intensity under field conditions. This is contrary to observations on other arctic plants in low arctic environments (Tieszen, 1973; Shvetsova and Voznessenskii, 1971) where photon flux density and soil moisture are more often limiting.

It was not possible to develop a relationship between field moisture regime and net CO$_2$ assimilation rate. The range of soil and leaf water potentials found in the field was very narrow. Soil moisture (0-5 cm) never dropped below −0.03 MPa and leaf water potential was rarely below −0.5 MPa during the season (Figs. 1 and 2).

With the onset of dieback, net assimilation rates dropped. Typical midday net photosynthetic rates ranged from 10-15 mg CO$_2$·g^{-1}·h^{-1} during much of the growing period, but dropped to 2-5 mg CO$_2$·g^{-1}·h^{-1} with the onset of senescence. Dark respiration was also lower (Table 3). The reduction of both net photosynthesis and dark respiration appears to represent a general slowing of plant metabolism with senescence.

Light and Temperature

There was a significant interaction ($p < .001$) between the

TABLE 3. Net assimilation rate (NAR) of *Luzula confusa* under environmental conditions before (28 July) and after (4 August) the onset of senescence. All values are averages of three samples.

Date	Photon Flux (µmol·m^{-2}·s^{-1})	Leaf Temperature (°C)	NAR (mg CO$_2$·g^{-1}·h^{-1})
28 July	274	3.7	4.4
	0	3.4	−2.3[a]
4 August	335	3.5	1.2
	0	2.8	−1.3

[a]Negative values indicate respiration in the dark.

responses of NAR to light and temperature within controlled environments. Light compensation of *L. confusa* was higher at high temperatures, and the broad thermal optimum was elevated at high photosynthetic photon flux densities (Fig. 6). The shift in thermal optimum appears to be an adaptation of the plant to maintain positive net assimilation in an environment where leaf temperatures are tightly linked to radiation load. Similar observations were made by Hartgerink and Mayo (1976) for *Dryas integrifolia* from Devon Island, N.W.T. In spite of the influence of photon flux density on temperature optimum, there was general agreement with other arctic plants (Tieszen, 1973; Tieszen and Wieland, 1975, Hartgerink and Mayo, 1976). Since the temperature optimum (15-25°C) was well above field leaf temperatures (5-8°C), NAR was strongly dependent on leaf temperature as shown above.
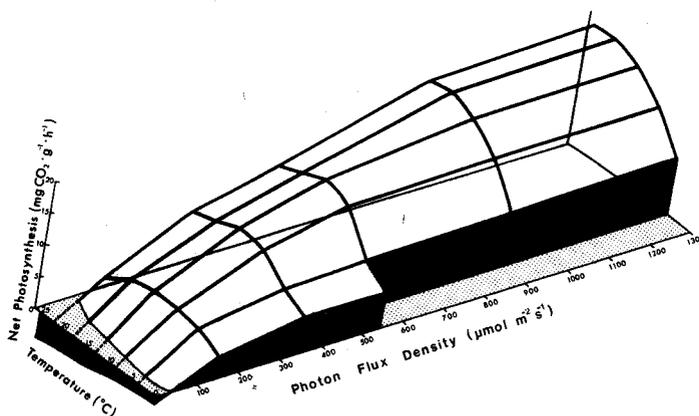
FIG. 6. Net photosynthesis of *Luzula confusa* vs. photon flux density and temperature under laboratory conditions. All values are means of 9-10 tillers from eight different plants.

The maximum NAR of 19-20 mg CO$_2$·dm^{-2}·h^{-1} was similar to that of other arctic graminoids (10-20 mg CO$_2$·dm^{-2}·h^{-1}; Tieszen, 1973) as was dark respiration (Table 4; Tieszen, 1973). The respiration rate, however, was lower than that of several other arctic and alpine shrubs and herbs such as *Chrysothamnus isidiflorus* (Mooney et al., 1964), *Dryas integrifolia* (Hartgerink and Mayo, 1976), and *Thalictrum alpinum* (Mooney and Johnson, 1965).

TABLE 4. Dark respiration and maximum net photosynthesis of *Luzula confusa* under laboratory conditions (mean and 95% confidence limits)

Temperature (°C)	Dark Respiration (mg $CO_2 \cdot g^{-1} \cdot h^{-1}$)	Maximum Net Photosynthesis (mg $CO_2 \cdot g^{-1} \cdot h^{-1}$)
0	1.0 ± 0.8	5.4 ± 2.0
5	1.4 ± 0.8	9.1 ± 3.4
10	2.0 ± 0.8	14.7 ± 0.7
15	3.0 ± 0.9	18.0 ± 2.1
20	3.0 ± 1.4	19.9 ± 1.9
25	3.9 ± 2.7	19.3 ± 1.8

Soil Water

Water balance did not appear to be a significant controlling factor for the metabolism of *L. confusa* on King Christian Island during the study period. In the laboratory, however, the response of NAR to Ψ_ℓ (Fig. 7) corresponded to that of alpine plants (Johnson *et al.*, 1974) and appeared to increase linearly with increasing water potential (NAR[mg $CO_2 \cdot g^{-1} \cdot h^{-1}$] = 29.85 + 0.036 Ψ_ℓ [kPa]; p < .001). Net assimilation rate decreased as Ψ_ℓ decreased, and was less than 25% of maximum at −0.7 MPa. This reduction was similar to that of *Calamagrostis breweri* (Klikoff, 1965) but much greater than for *Carex exerta* (Klikoff, 1965); *Dryas integrifolia* (Hartgerink and Mayo, 1976); and *Kobresia myosuroides, Geum rossii*, and *Deschampsia caespitosa* (Johnson *et al.*, 1974). Most of those species, however, are native to more xeric environments than is *L. confusa*.
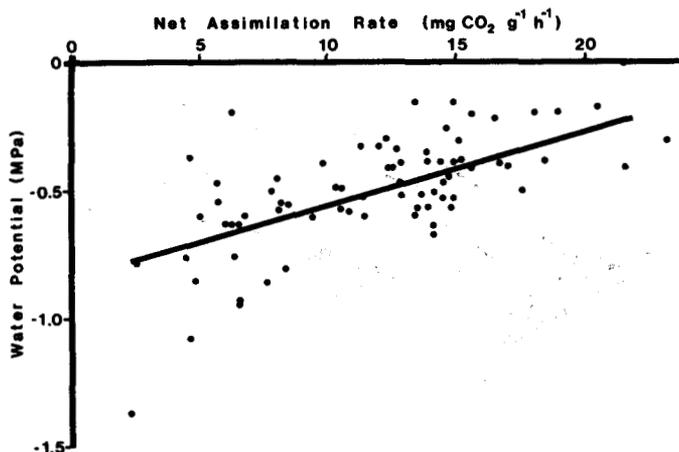
FIG. 7. Linear regression of net assimilation rate of *Luzula confusa* vs. leaf water potential under laboratory conditions.

Phenology

Phenological stage was shown to have a great impact on NAR. Maximum NAR ranged from 16 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ (540 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD @ 10 °C) at anthesis to 5 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ during senescence (Fig. 8). The trend in NAR was to increase to a maximum at anthesis and gradually decrease as the plant approached dormancy. The lower values of NAR before flowering (Fig. 8) were likely the result of higher respiration rates during growth (Bliss, 1966; Tieszen and Wieland, 1975). Reduced NAR after flowering appeared to represent a general slowing of plant metabolism that was also seen in the field. The slowing of both rates with the onset of dormancy has been shown in *Dryas integrifolia* (Hartgerink and Mayo, 1976). The leaves of *L. confusa* mature rapidly and show positive net carbon assimilation early in the season (Fig. 8). The importance of rapid growth and maturation of graminoid leaves has been emphasized by the simulation studies of Miller and Tieszen (1972) at Barrow, Alaska.
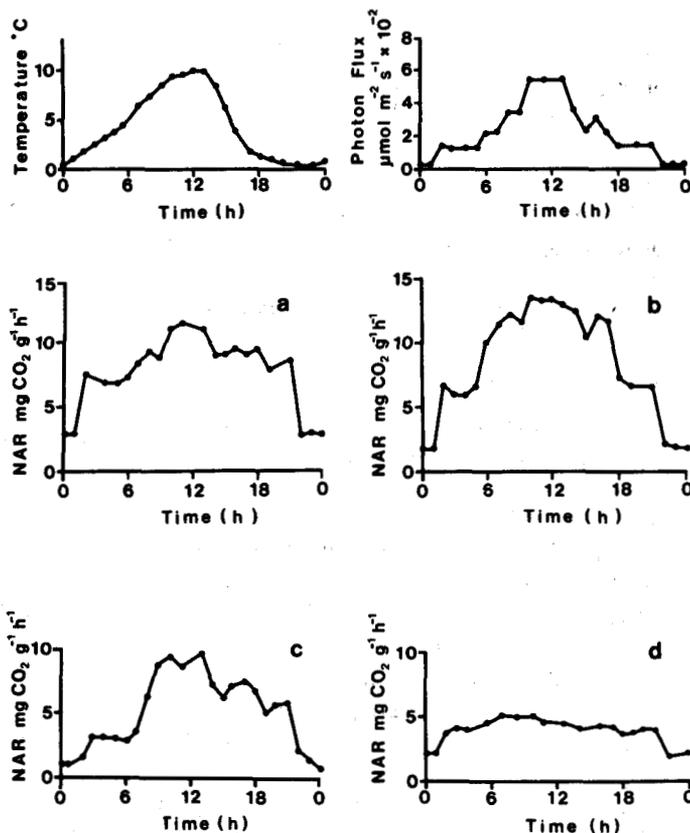
FIG. 8. Net assimilation rate of *Luzula confusa* at four phenological stages in laboratory; (a) pre-flowering, (b) anthesis, (c) post-flowering, and (d) dieback. Light and temperature conditions during measurement and growth are also given.

Simulation Studies

An empirical model which used NAR regressed against temperature above 3 °C and NAR regressed against photosynthetic photon flux density (PPFD) below 3 °C was tested using NAR, leaf temperature and PPFD measurements from a day with moderately high incoming radiation (28 July 1975). The data from this day were not used in the regression analyses. The agreement between predicted and measured values (Fig. 9) was close, and the prediction of daily average NAR was within 1 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ of the measured daily average (6.9 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$). Under cloudy conditions (1 August 1975), the difference in daily NAR between predicted and measured daily rates was also low (1.3 vs. 0.9 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$).
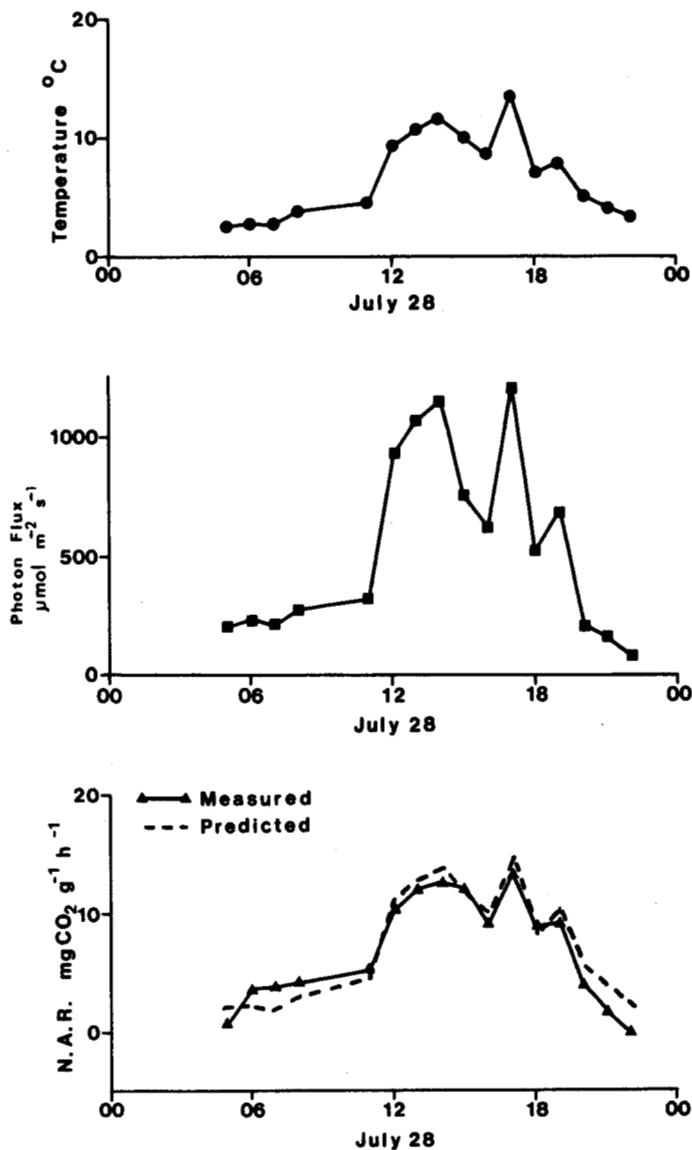
FIG. 9. Net assimilation rate of *Luzula confusa* and environmental conditions during 28 July 1975.

FIG. 10. Comparison of predicted *vs.* measured values of net assimilation rate under laboratory conditions.

may have acclimated to the lower photosynthetic photon flux densities under which they were grown in the environmental growth chambers. This might account for the higher NAR at low PPFD and the lower NAR at higher PPFD as compared with field plants. The ability of arctic and alpine plants to acclimatize to growing conditions is well known (Billings *et al.*, 1971). The lower-than-predicted NAR may also be a result of low soil temperatures (Bliss, 1966). The empirical nature of the model makes it virtually impossible to use it except under the narrow range of plant and environmental conditions under which it was derived. This is illustrated by the poor predictive capabilities of the laboratory model under field conditions.
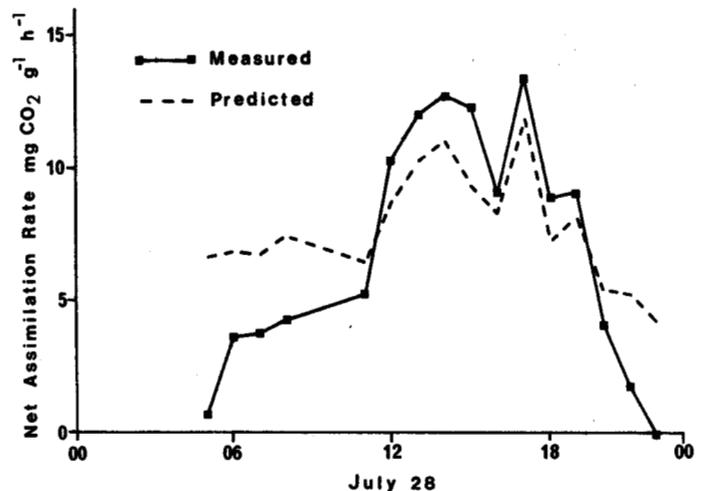
FIG. 11. Comparison of net assimilation rate predicted using laboratory model and field conditions, and that measured under field conditions.

A second empirical model was developed from laboratory-derived responses of NAR to leaf temperature, PPFD, and leaf water potential. The model predicted values of NAR that fell between laboratory measurements for before and after flowering phenological stages (Fig. 10). Much of the difference between predicted and measured values can be accounted for by variability among individual plants and by the fact that phenology was not taken into consideration when responses of NAR to PPFD, temperature, and water were determined. The model therefore appeared to be capable of estimating NAR of an "average" *L. confusa* plant in the laboratory.

In the field, the model based on laboratory responses was not as effective as it was in the laboratory, and the difference between measured and predicted NAR was substantial (Fig. 11). The model overestimated NAR at low PPFD and temperature and underestimated NAR at high PPFD and temperature. The reason for discrepancies between predicted and measured values is not known, but it is thought that the laboratory plants

The model of NAR, based on single factor analysis and derived from field data, appeared to be much more accurate (cf. Fig. 9) and was used to predict the photosynthetic capability of *L. confusa* in the King Christian Island environment. Although it was not possible to calculate production of *L. confusa*, because live standing crop was not measured throughout the season, Figure 12 shows that the potential for net photosynthesis was much higher in spring and early summer than in late summer. This illustrates the importance of im-

mediate initiation of growth in spring that is characteristic of *L. confusa*. Growth was initated within two days of snowmelt, and since time of melt was usually in late June or early July, *L. confusa* took advantage of the best available conditions for net photosynthesis. Rapid production of green material was made possible by preformed buds and partially extended green leaves that persisted over winter. The utilization of the moss layer as a rooting medium (6.6% of *L. confusa* root standing crop, Table 2) also appears to be necessary for rapid initiation of growth in spring, since water needed for elongation would not be available from frozen mineral soil.
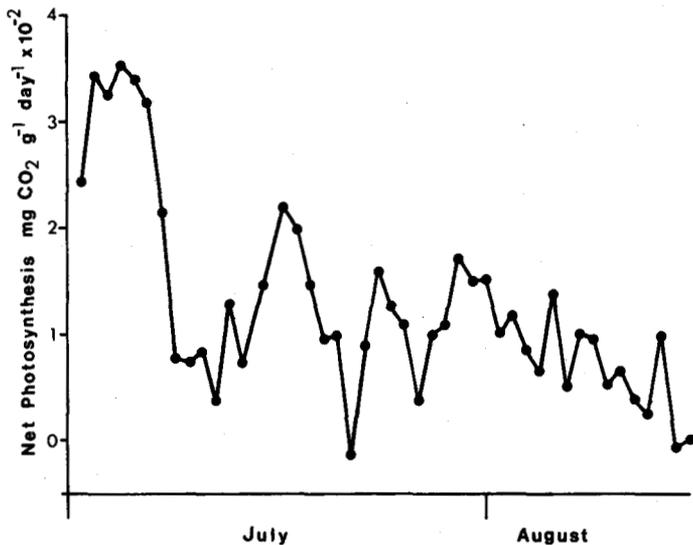
FIG. 12. Potential net photosynthetic rate (field model) based on actual field conditions during summer 1973.

ECOLOGICAL IMPLICATIONS

Low summer temperature appears to be the dominant environmental factor responsible for the low growth rate of plants in arctic environments (Tieszen, 1972; Billings, 1974). In spite of the tufted growth form of *L. confusa*, which tends to ameliorate the thermal regime, temperature still appeared to be the most influential factor on plant growth. Leaf temperature was generally 1-2°C above ambient air temperature during the 1973 growing season on King Christian Island (Addison and Bliss, 1980). Although this difference was small when compared to plants at other high arctic sites (Warren Wilson, 1957; Addison, 1977), it appeared to have a substantial influence on net photosynthesis. The field model of net photosynthesis estimated a 250% increase in NAR with a 1°C rise in temperature at 3°C (1.0 *vs.* 3.5 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$). In general, both photosynthesis and dark respiration operated at low temperatures, and positive net photosynthesis was observed at leaf temperatures of −2°C to −3°C, both in the field and in the laboratory. Both above- and below-ground temperatures are important in plant functioning, but growth and development of arctic and alpine plants are affected more by soil than by air temperatures (Bliss, 1966; Dennis and Johnson, 1970). Over 80% of *L. confusa* roots were in the surface 5 cm of soil, and this morphological adaptation to utilize the warmest soil environment is probably extremely important for the success of the species.

Water did not appear to be limiting for the survival of *L. confusa* on King Christian Island during the summers of 1973-1975. The high water potential in the soil ($\Psi_{soil} > -0.03$ MPa) and high atmosphere humidity (VPD < 0.05 kPa) permitted a shallow soil-to-leaf water potential gradient to be adequate to supply the plant with

TABLE 5. Comparison of characteristics of high arctic plant species

Characteristic	*Dryas integrifolia*	*Carex stans*	*Luzula confusa*
Growth form	Cushion	Upright Graminoid	Tufted Graminoid
Plant age (years)	20 - 120	5 - 7[b]	90 - 130
Root-to-shoot ratio	0.4 - 0.6	9 - 13	0.3
Leaves produced annually	2	2 - 3	2
Leaves function (year)	2	1+	2
Leaf area index (plant basis)	1.0	2.4	1.4
Net photosynthesis (average) (mg $CO_2 \cdot g^{-1} \cdot h^{-1}$)	2 - 3	11 - 15	10 - 15
Shoot dark respiration (average, mg $CO_2 \cdot g^{-1} \cdot h^{-1}$)	1.5	1.6	1.4
Leaf water potential (average, MPa)	−3.2	−1.4	−0.5
Leaf resistance (sunny day) (s·cm^{-1}) (calculated)	20	16	3
Drought resistance	High	Low	Low
Energy regime (% of net radiation)			
Latent heat flux	15	52	28
Sensible heat flux	83	39	63
Soil heat flux	2	9	9
Leaf temperatures above ambient (°C)			
Sunny	15-20	5-10	5-8
Cloudy	0-5	0-2	0-2

[a]From Addison (1977), Mayo *et al.* (1977), Muc (1977) and Svoboda (1977) summarized by Bliss (1977).

[b]Individual shoot.

water. The average Ψ_ℓ of *L. confusa* was greater than -0.5 MPa and turgor was usually greater than 0.6 MPa. On the rare occasions when turgor was low (<0.1 MPa), transpiration rates were greatly reduced, owing to the increase in leaf resistance from the normal 1-2 s·cm^{-1}. The laboratory experiments showed that net assimilation dropped dramatically (25% of maximum) when Ψ_ℓ decreased to only -0.7 MPa. In the unusually cold and dry summer of 1979, soil water potential (2-5 cm depth) dropped to -1.7 MPa in mid-July and to <-7.0 MPa after 30 July (Grulke, 1983). Should two or more warm, dry summers occur consecutively, large areas of *Luzula confusa* and probably *L. nivalis* might be severely affected.

L. confusa appeared to be better able to resist water deficit at the end of the growing season than at the beginning, owing to the lower elasticity of the cell walls that resulted in a more sensitive control of water flux. However, the plant did not demonstrate a capability to withstand severe water deficit as compared with more xeric species from the same experiment (Grulke, 1983). This helps to explain why *Luzula confusa* and *L. nivalis* are confined to more mesic habitats on this and other northwestern islands (Bliss and Svoboda, 1984).

Several other characteristics of *L. confusa* appeared to be important for survival and growth in the King Christian Island environment (Table 5). *L. confusa* appeared to combine the higher photosynthetic capacity of the upright graminoid (*Carex stans*) with the energy-trapping features and longevity of the cushion plant (*Dryas integrifolia*). It is felt that the low leaf area index and non-drought-resistant nature of *L. confusa* may be the costs that go with both metabolic and physical energy efficiency. Many of the plant characteristics such as low root-to-shoot ratio, low leaf temperature, high water potential, and low leaf resistances (Table 5) are adaptive responses to this tufted graminoid to the low temperature and radiation on King Christian Island (Addison and Bliss, 1980) as compared with the upright graminoids in the higher temperature and radiation on Devon Island (Courtin and Labine, 1977).

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