ADAPTATION IN TUNDRA PLANTS EXAMPLIFIED BY TRANSPLANTATION STUDIES AT TWO LATITUDES

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Abstract: Transplantation studies between Spitsbergen (78°55' N) and the Dovre mountains in southern Norway (62°14' N, *ca.* 1100 m a.s.l.) are carried out on three species (*Carex rupestris, Luzula confusa* and *Polygonum viviparum*), naturally growing in both ecosystems. Growth of the first two species is also studied at various temperatures and day lengths in a phytotron.

At both field sites the leaves of the Spitsbergen plants started to die much earlier than those of the Dovre plants. However, the leaf bases of the two monocotyledons at both sites partly stayed green through the whole winter. Also in the phytotron, at low temperatures the monocotyledons from Spitsbergen ended their growth significantly earlier than the plants from Dovre both on short and long days, while the difference was small at somewhat higher phytotron temperatures. The plants from Spitsbergen were generally larger than the plants from Dovre during the phytotron experiment, independent of the growing temperature and the light conditions. However, when grown in the field at Spitsbergen, plants from Dovre, particularly *Luzula confusa,* showed stronger new green growth than the native plants from Spitsbergen. At Spitsbergen, plants of *Polygonum viviparum* from Dovre were taller than those from Spitsbergen. The Dovre population has more vertical, but significantly narrower leaves than the arctic population.

The functional adaptations to growth in low temperatures and in different light climates are discussed.

1. Introduction

Polar and alpine tundra plants are adapted to a short growing season by having very rapid growth, although some species may take several years to finish the life cycle from the initiation of flower primordia to ripe seeds (RESVOLL, 1917). Several species show positive net assimilation even from before all the snow is melted, because of penetration of sunlight through up to about 50 cm snow cover (WIELGOLASKI, 1987), dependent on the consistency of the snow. Plant growth under the snow takes place, of course, only if the upper soil layer is not frozen, but this is often the case in late winter after a good snow cover. The growth explosion in spring is mostly an elongation of small leaves initiated the previous fall.

In some cases growth continues also below 0°C air temperature, often down to −4 to −5°C in vascular plants (PISEK *et al.,* 1967; MOSER, 1969; LARCHER *et al.,* 1975; TIESZEN *et al.,* 1980), in some northern cryptogams even at lower temperatures (KALLIO and KÄRENLAMPI, 1975). They found the lichen *Cetraria nivalis* to continue growth

down to nearly −20°C in subarctic Finland.

The photosynthetic optimum temperature in some lichen species, for instance in a Spitsbergen strain of *Stereocaulon paschale* (LANGE, 1965), is close to 0°C, an amazing adaptation to arctic conditions. Similar results have also been found for various species of mosses as well as for some higher plants. However, TIESZEN *et al.* (1980) observed temperature optima of leaf photosynthesis between 10 and 15°C for several phanerogams in arctic North America. The optima temperatures for several tundra mosses are from 10 to nearly 20°C. For instance there was found an optimum temperature of 10°C for *Dicranum elongatum* and *Polytrichum juniperinum* (KALLIO and KÄRENLAMPI, 1975), but only 5°C for the moss *Racomitrium lanuginosum* sampled from various parts of the world. Even if the optimum temperature is higher, considerable net photosynthesis may continue close to 0°C; for instance the moss *Pogonatum* is found to photosynthesize at 55% of the maximum rate at 0°C (TIESZEN *et al.*, 1980).

There is an important link between life forms and ecological functions. Polar vegetation is extremely sensitive to small variations in temperature. The leaf structure influences light interception as well as heat interception from the ground and also heat loss from the plants.

The greatest solar interception per unit leaf area and highest leaf temperatures is generally found when radiation reaches the leaves at a right angle. In many parts of the world leaf temperatures are then too high for optimal growth. At high latitudes, however, the solar angle is low and temperatures are often below optimum, at least in moist situations. This means that the presence of vertical leaves in polar tundra may increase their production.

Many tundra species do have several nearly vertical leaves, especially monocotyledons (Fig. 1, left). It is not surprising that high net photosynthesis is found in single-shooted monocotyledons at high latitude (TIESZEN *et al.*, 1981), where the shading effect is moderate even for the inner, nearly vertical leaves. As this life form in tundra normally grows in very wet conditions, the leaf temperature seldom is overoptimal, even on the upright unshaded leaves, because of cooling by transpiration. This may explain why this life form is favored by the low solar angle at high latitude when the soil moisture is high enough.

Some tundra plants, however, have nearly horizontal leaves. This means a de-
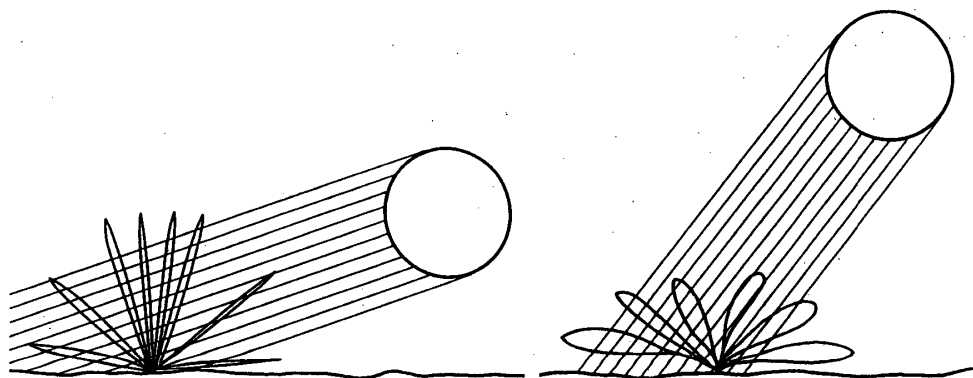

Fig. 1. *Steeply inclined leaves increase the solar interception at low solar angles (high latitudes) (left), while more horizontal leaves increase the interception at higher solar angles and the interception of heat from the soil (right) (WIELGOLASKI, 1984).*

crease in solar interception at the low sun angles at high latitudes compared to lower latitudes (Fig. 1, right).   Leaves near the soil surface, on the other hand, always recieve a heat surplus from the ground during the day, particularly if the soil is dry.   Many tundra plants in such environments are protected against overheating by accumulation of several dead leaves between the living ones, remaining for several years due to the slow decomposition rates at the low temperatures.   This is the case in *Dryas* spp. and in other cushion plants, in most plants with appressed rosettes, and in tufted monocotyledons.   However, if the most important growth period is in early spring just after snow melt (*i.e.* before the soil has dried), then an increased temperature from the soil surface may be favorable to the tundra plants.   Species such as *Oxyria digyna* and *Ranunculus glacialis* are examples of tundra plants with leaves which are nearly horizontal, particularly in spring.

The dead leaves also protect the plants against water loss.   This effect is increased by the often small leaves of arctic plants and development of a dense hair layer.   This helps to store the incoming heat as well.   Crowberries (*Empetrum*) of the low and middle arctic, for instance, have very small leaves, while, for instance *Cerastium alpinum* with a wide habitat tolerance in the whole arctic, has hairy leaves.

Adaptation to the short growing season in the arctic (often less than eight weeks) and low average growth temperatures (commonly less than 5 °C) may explain the large proportion of live nongreen biomass compared to green biomass, as is often found in tundra.   As a great amount of the storage carbohydrates is found in roots in graminoids (grasses and sedges), this often means a great root biomass compared to the top in these plants (Table 1).   In forbs much of the storage material may also be found in roots and then the same is true as for graminoids, but the main storage of forbs may also be in the shoot basis.   Woody plants (trees and shrubs of all types) store as much material in woody aboveground parts as in roots.   Translocation (transport of carbohydrates and nutrients) takes place most strongly in fall and early spring, between storage organs and growing points, particularly roots (CHAPIN and SHAVER, 1985).   This transport and transformation, however, demands considerable energy.

Table 1.   Average ratios of tundra phytomass in some vegetation types (WIELGOLASKI et al., 1981).

Region	Shoot to root (live)	Green to nongreen live vascular plants	Live to dead aboveground vascular plants
Desert and semi-desert	1 : 0.9	1 : 2.3	1 : 1.9
Wet sedge meadows	1 : 21	1 : 23	1 : 1.6
Mesic-dry meadows	1 : 5.0	1 : 7.7	1 : 0.8
Dwarf shrub tundra	1 : 3.1	1 : 12	1 : 0.6
Low shrub tundra	1 : 2.0	1 : 19	1 : 0.2
Forest tundra	1 : 0.8	1 : 15	1 : 0.1

In extreme climatic conditions sufficient energy may not be available to support both the storage and translocation systems.   Plants, for instance in the high arctic and polar desert, therefore are often adapted to reduce the translocation by keeping some of the leaves green all the year.   This is the case for many of the polar desert forbs, grasses and sedges, which do not have the high root mass compared to tops that are observed in the less extreme lower arctic regions.   Instead, the energy and nutrients are stored in the leaf bases which are often evergreen, although the leaf tips are normally dead.   It is

observed that in the Canadian high arctic tundra the lower parts of leaves in the middle of densely tufted *Carex nardina* live 4 to 6 years (SVOBODA, 1977). In some plants in the polar deserts many leaves are reddish in winter, but do not die. These leaves then turn rapidly green again in spring when new chlorophyll is synthesized. At lower latitudes the leaves normally die during winter in the same species. This is found for instance in *Dryas* and in some *Saxifraga* growing on exposed rocky cliffs. Similar adaptations are found in *Juncus trifidus* and in *Kobresia myosuroides* in plants growing on exposed ridges.

It is observed that leaves of evergreen dwarf shrubs, common in dry, nutrient poor and wind swept ridges in the low arctic, remain active for 2–3 years (FLOWER-ELLIS, 1975; CALLAGHAN and COLLINS, 1981). Shrubs close to their border for survival have to be low and creeping to be protected by some snow cover against the lowest temperatures, but also not to be too strongly exposed to wind. In the extreme high arctic the conditions are normally too harsh for the aboveground reserves in woody parts and buds of even evergreen dwarf shrubs. This is probably why all shrubs normally are missing here.

When the leaves stay more or less green in winter, the plants may not need to transport carbohydrates and mineral nutrients from and to the leaves in fall and spring, respectively, and thus save energy. They can also utilize the radiation from early spring for photosynthesis in the old leaves (TIESZEN *et al.,* 1981). Therefore, evergreens often have a late bud break in spring. But nutrients may be moved from old leaves to the new growth places when this is needed. This internal nutrient circulation may be seen as an . adaptation in evergreen plants to grow on nutrient poor soil.

Some of these adaptations are observed in the present transplant studies carried out on three species in experiments in alpine southern Norway and Spitsbergen, and in a phytotron on two of the same species.

2. The Sites, Material and Methods

The plant species *Carex rupestris, Luzula confusa* and *Polygonum viviparum* were transplanted between the low alpine region at about 1100 m elevation at the Dovre mountains in southern Norway (62°14′N) and the mid-high (or northern) arctic region (ELVEBAKK, 1985) of Ny-Ålesund on Spitsbergen (78°55′N). The community at the site at Dovre was a *Loiseleuria heath* (Loiseleurio-Diapension according to DANIËLS, 1982), which indicates an acid soil substrate (DAHL, 1956). This is also shown by the presence of *Luzula confusa* near the site, although growth of *Polygonum viviparum* and the close vicinity to *Carex rupestris* indicate some eutrophication (ELVEBAKK, 1982). The vegetation at the Spitsbergen site was dominated by *Carex rupestris* and *Dryas octopetala* (Rupestri-Dryadetum according to RØNNING, 1965), indicating a more calcareous material than at Dovre, although *Luzula confusa* was also found at the Ny-Ålesund site.

Because of the variation in latitude between the two sites there are of course great differences in day lengths between the sites. At Ny-Ålesund there are 24 hour days from late April to late August, while the days are never more than 19 hours long at Dovre (Fig. 2). The temperatures through the various months of the year are generally
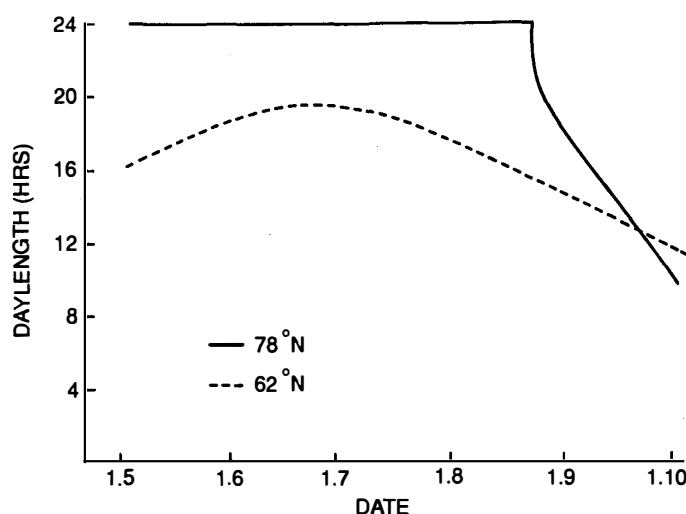
Fig. 2. Daylengths during summer at 62°N and 78°N given as
number of hours when the sun is above the sea level.

higher at Dovre than at Ny-Ålesund, and due also to the proximity to the sea, the summer temperatures are always relatively low at Ny-Ålesund.

Plants were dug up near the alpine Dovre site and near the arctic Ny-Ålesund site. They were brought to the other site with some soil and planted as soon as possible. Transplantations were also carried out within each site to eliminate a transplantation effect in the growth studies.

There were several shoots of Carex rupestris on the root stem of one plant.   A unit of 2–4 shoots from the youngest part of the root stem was used.   The unit of Luzula confusa was 3–5 shoots from one tussock. In Polygonum viviparum a unit was the plant belonging to one rootstock.   The plantations were arranged in a block experiment (4 blocks), each block by 10 replicates at Spitsbergen and 5 replicates at Dovre.   The planting took place in June, except for the plants from Spitsbergen to Dovre which were planted in August.   The sites were fenced against grazing by large mammals.   In all plants the flowers were removed and for Polygonum also the bulblets, to make sure that there should be no mixing of populations.   Growth of the plants was studied through one season (the year after transplantation).   After the studies all plants were removed from the sites.

The two monocotyledons were also studied in a phytotron after cold treatment (freezing at $-15\,°C$ for one month).   In the phytotron all the plants were grown in fertilized standard soil at different temperature and light conditions as shown in Table 2. The highest temperatures were said to simulate the conditions at Dovre and the lowest

Table 2. Values used in phytotron studies of low ("Spitsbergen") and high ("Dovre") temperatures and of light intensities on long days ("Spitsbergen") and short days ("Dovre").

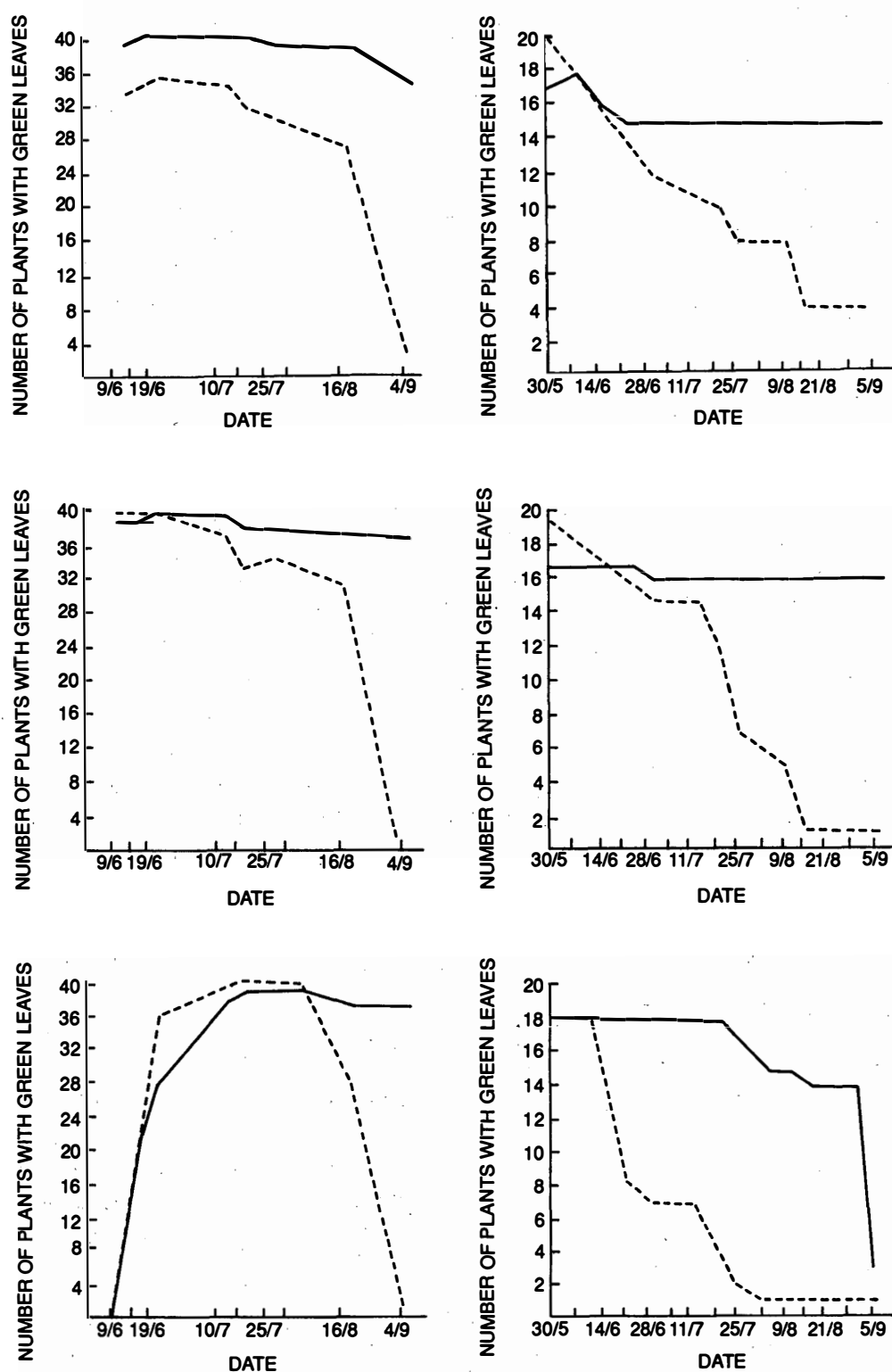|	Temperature (°C)		Light (lux)	
	Night (6h)	Day (18h)	Night (6h)	Day (18h)
"Dovre" temp. and "Dovre" light	7	17	0	20000
"Dovre" temp. and "Spitsbergen" light	7	17	300	20000
"Spitsbergen" temp. and "Dovre" light	4	9	0	20000
"Spitsbergen" temp. and "Spitsbergen" light	4	9	300	20000

Fig. 3.   Number of plants with green leaves for an arctic population (broken line) and an
          alpine population (solid line) when grown at Spitsbergen (left) and Dovre (right).
          Upper row Carex rupestris, middle row Luzula confusa and lower row Polygonum
          viviparum.

temperatures the conditions at Spitsbergen. All temperatures, however, used in the phytotron were somewhat higher than the values observed at the sites, but it was impossible to obtain lower temperatures in the phytotron during light hours than the ones used to simulate the Spitsbergen climate.

The numbers of new green leaves were counted and the lengths of these leaves measured at Spitsbergen and in the phytotron at approximately weekly intervals. The numbers of shoots were counted in the two monocotyledons, while the widths of the leaves and the heights of the plants were measured in *Polygonum* at Spitsbergen. The length of the growing season and the death rates were observed in all experiments.

3. Results and Discussion

The populations from Spitsbergen of all three species wilted much earlier in the fall than the Dovre populations, both when grown at Spitsbergen and at Dovre. However, in all three species the wilting of the Spitsbergen populations started earlier at the Dovre site than at Spitsbergen (Fig. 3). According to NILSEN (1986) an increased amount of incoming far red light compared to red in the fall and particularly at lower latitudes is of great importance to induce an early stop in plant growth in arctic populations. Therefore, plants from Spitsbergen may wilt earlier when grown at more southerly latitudes, as for instance Dovre, with a higher proportion of far red light.

There was a clear difference, both between the populations (Dovre and Spitsbergen) and the treatments, in the average leaf length in the phytotron studies (Table 3). In the Dovre populations the leaf growth continued through a significantly longer period than in the Spitsbergen populations and particularly at the highest temperature. The day length seems to have little influence. This suggests an ecotypic adaptation to the generally lower temperatures at Spitsbergen. The critical day length for this growth parameter may be shorter than the 19 hours during summer at Dovre and has, therefore, less influence on the average leaf length.

Table 3. *Leaf length (cm) per leaf in an arctic (Spitsbergen) and an alpine (Dovre) population of* Carex rupestris *and* Luzula confusa *grown in a phytotron at various temperatures and daylengths (cf. Table 2) through 40 and 88 days.*

	"Dovre" temp. "Dovre" light		"Dovre" temp. "Spitsb." light		"Spitsb." temp. "Spitsb." light		"Spitsb." temp. "Dovre" light	
	40d	88d	40d	88d	40d	88d	40d	88d
C. rupestris, alpine	3.9	4.8	2.7	4.9	2.7	2.8	2.0	2.1
C. rupestris, arctic	2.4	2.3	2.3	3.0	1.5	1.7	1.2	0.8
L. confusa, alpine	2.8	4.1	1.6	3.4	1.5	3.2	2.2	3.4
L. confusa, arctic	2.1	2.6	2.7	2.6	2.8	1.7	2.2	1.8

However, the production of new leaves continues longer in long days than in short days at low temperatures. In the phytotron it was observed that the Spitsbergen population of *Carex rupestris* produced new leaves through nearly three months when grown at low temperatures and long days, but only through half as long a period when grown in short days (Fig. 4, left). This suggests that the various growth parameters have different responses to temperature and day length.

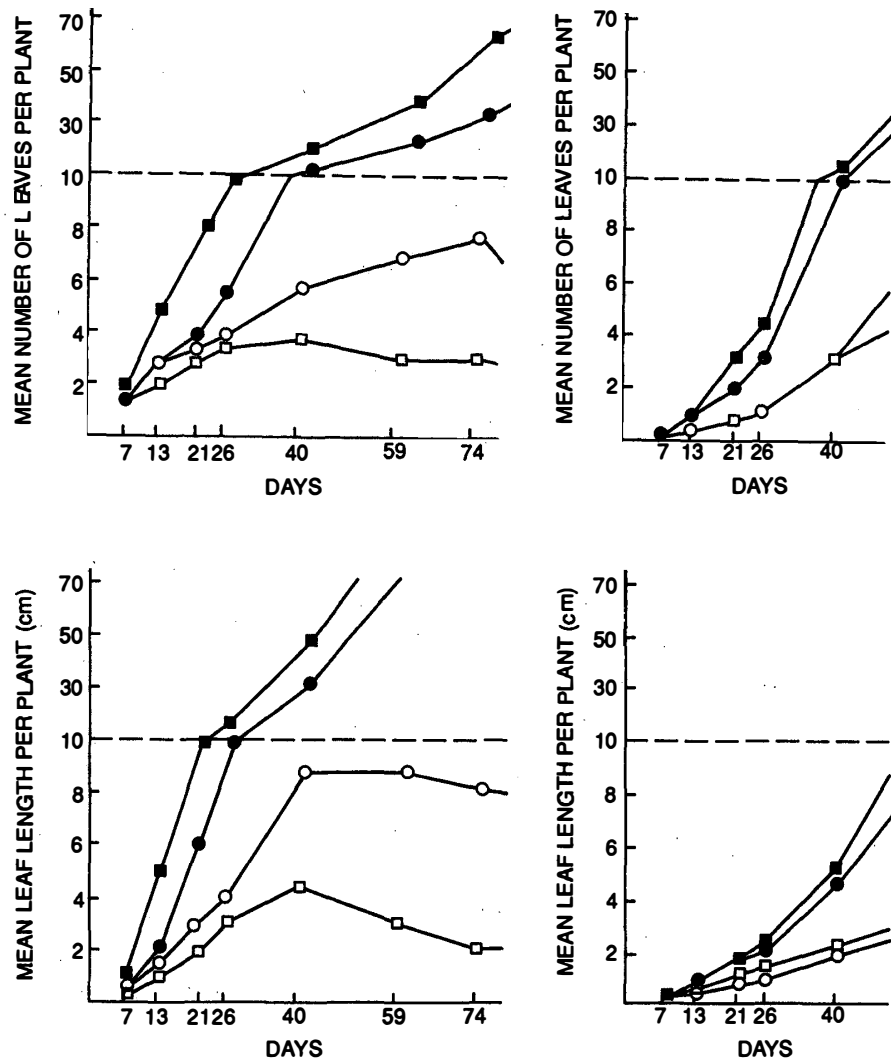In the phytotron the Spitsbergen population (Fig. 4, left) of *Carex rupestris* also

Fig. 4. Number of new green leaves (upper row) and sum of green leaf length (cm)
(lower row) of an arctic (left) and an alpine (right) population of Carex
rupestris through the growth period (days) in a phytotron at various
combinations of light and temperature (cf. Table 2).
"Dovre" temperature and "Dovre" light ■.
"Dovre" temperature and "Spitsbergen" light ●.
"Spitsbergen" temperature and "Dovre" light □.
"Spitsbergen" temperature and "Spitsbergen" light ○.

first stopped growing when cultivated at low temperature, more or less independent of
the day length.   In Salix polaris it has been shown that the temperature has a significant
influence on leaf abscission (PAUS et al., 1986).   In a Spitsbergen ecotype of the species
they found a stimulation in leaf shedding by low temperature, independent of the day
length (although the shedding was stimulated by short days at higher temperature),
while in a more southern latitude ecotype of the same species the leaf abscission was
enhanced by short photoperiods even at low growth temperature (6°C).

In the phytotron the Spitsbergen population of the two monocotyledonous species
showed significantly ($P<0.05$) faster growth than the Dovre populations.   This was
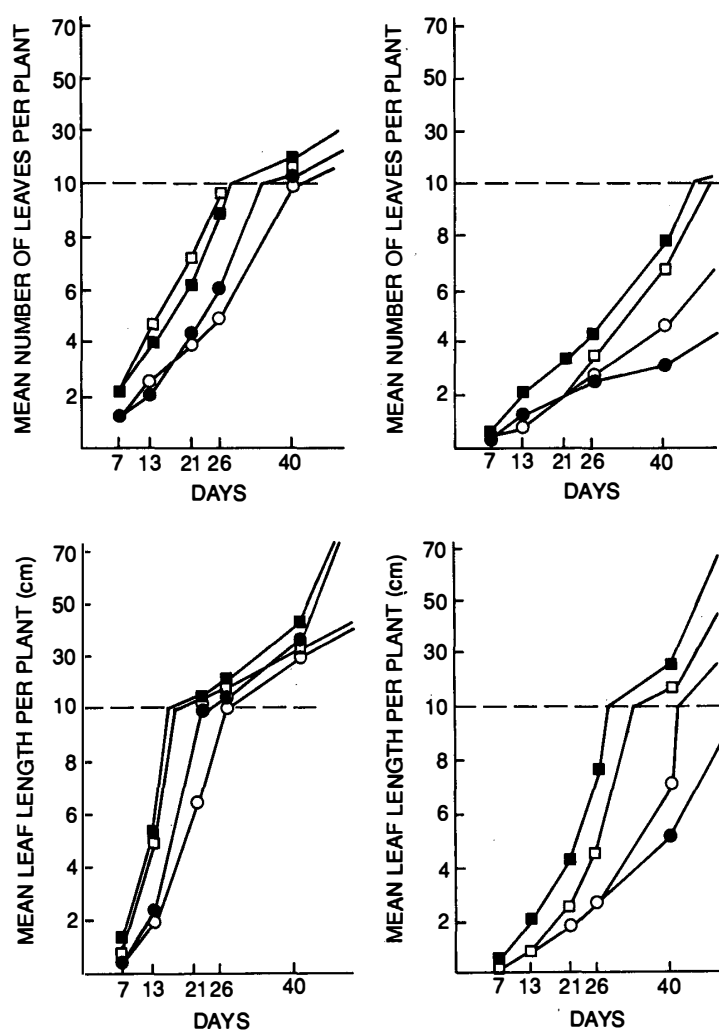expressed both in the number of leaves and in the sum of new green leaf length (Figs.

Fig. 5. Number of new green leaves (upper row) and sum of green leaf length (cm) (lower row) of an arctic (left) and an alpine (right) population of Luzula confusa *through the growth period (days) in a phytotron at various combinations of light and temperature (cf. Table 2). Symbols as in Fig. 4.*

4 and 5). In *Carex rupestris* high temperature seemed to mean more for a rapid growth start than the day length, although short days might have been preferable at the highest temperatures. In *Luzula confusa* short days seemed to mean more than the temperature to obtain a good start of growth. The increased growth observed in the phytotron of the Spitsbergen population may be explained by a faster photosynthetic rate in the arctic population. If so, this is in accordance with BILLINGS *et al.* (1971) who found higher maximum net photosynthetic rates in the arctic than in alpine populations of *Oxyria digyna,* particularly after cold acclimation.

In the field at Spitsbergen particularly *Luzula confusa* showed significantly $(P < 0.01)$ faster growth (both in number of leaves and in sum of new green leaf length) in the Dovre population than in the native Spitsbergen population (Fig. 6). This is in accordance with results reported by SHAVER *et al.* (1986) and by CHAPIN and CHAPIN (1981) in reciprocal transplantations at 5 localities at various latitudes of *Eriophorum*
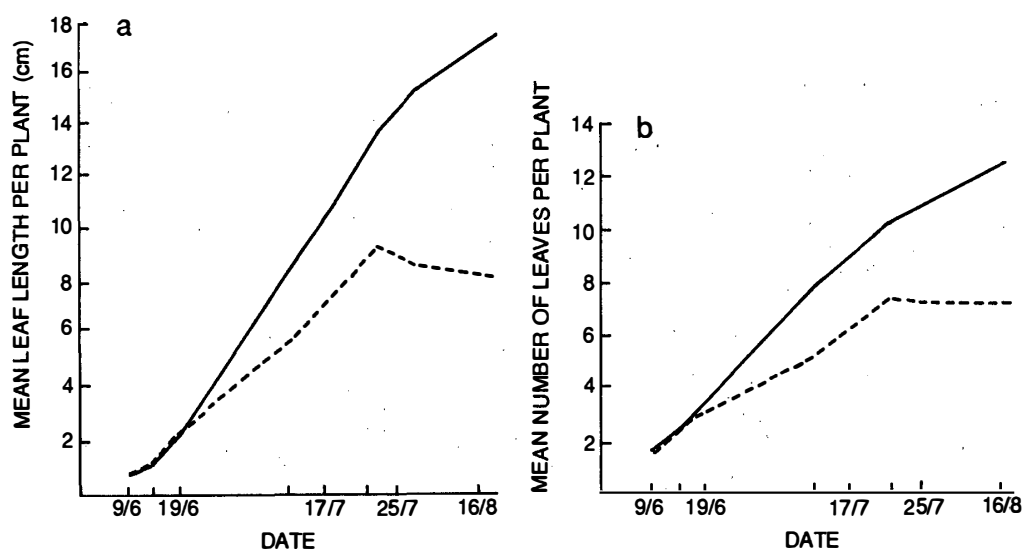
Fig. 6. Growth during the summer at Spitsbergen of an arctic population (broken line) and an
alpine population (solid line) of Luzula confusa. Left (a) sum new green leaf length
(cm), right (b) number of new green leaves.

vaginatum and Carex aquatilis populations, respectively. At first glance this seems to be
contradictory to the results from the phytotron reported above, but it may have
something to do with the light intensity in relation to day length. For instance, HAY
and HEIDE (1983) have found increased production in some perennial grasses of
northern origin by photoperiod extension, when the daily amounts of incident light
energy were the same. HEIDE (1985) explained the increased growth rate at extended
day length primarily by increases in net assimilation rates followed by increases in leaf
area ratios. However, in the present studies there is also a possibility that better soil at
the Ny-Ålesund site than at Dovre has caused better growth in the Dovre population
when transplanted to Spitsbergen. The growth differences may further be due to
temperature effects. The present results in the phytotron and in the field, respectively,
show the complexity in plant growth in relation to the environment.

Leaf widths were measured only in plants of Polygonum viviparum and only at
Spitsbergen. The native Ny-Ålesund population showed significantly wider leaves than
the Dovre population causing lowest leaf length–leaf width ratios in the Spitsbergen
population (Table 4). At the same time the Dovre population had more vertically
oriented leaves, and thus taller plants, than the Spitsbergen population. Because of the
low solar angles in the arctic it might have been expected that the Spitsbergen population
was adapted to this by having more vertical leaves than the Dovre population (cf.
WIELGOLASKI, 1984 and Fig. 1). The opposite result in the present studies probably had
something to do with the temperature conditions. The more horizontal leaves absorb

Table 4. The ratio at three dates of sum leaf length and sum leaf width in two
populations (arctic and alpine) of Polygonum viviparum grown at
Ny-Ålesund.

	June 19	July 17	July 31
Arctic population (Spitsbergen)	3.55	2.66	2.60
Arctic population (Dovre)	4.45	3.56	3.58

higher amounts of heat from the soil. This might be important for *Polygonum viviparum* under the climatic conditions at Spitsbergen, while the temperatures may be overoptimal at Dovre for the plants of the species, and therefore they show near vertical growth. The wider leaves in the species of the Spitsbergen than the Dovre population may be seen as a compensation to the more horizontal orientation of the leaves in collecting the incoming radiation for photosynthesis.

In the two other species studied, the monocotyledons, the leaf inclination was not measured, but it seemed as if the leaves of each shoot were more erect in plants of the Spitsbergen than of the Dovre population. This caused a problem in looking into the center of each shoot in the Spitsbergen monocotyledonous plants, while this was easier in the Dovre plants. This may be the reason why it was easiest to see a green leaf basis during winter in the Dovre plants of *Carex rupestris* and *Luzula confusa*. However, both species of both populations clearly had green leaf bases at both sites, which gave the plants an opportunity to start new photosynthesis early in spring without spending much energy on translocation from other storage organs. The old leaves with green bases in the present study seemed to die when new leaves were produced later in the season. This means that the green material in these plants probably did not last for several years, which is otherwise often observed in plants under extreme climatic conditions (SVOBODA, 1977).

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