Rev Environ Sci Biotechnol (2007) 6:33–45
DOI 10.1007/s11157-006-0014-z

REVIEW PAPER

Some views on plants in polar and alpine regions

F. E. Wielgolaski · S. R. Karlsen

Received: 7 March 2006 / Accepted: 9 June 2006 / Published online: 6 October 2006

Abstract Many plants growing in polar and alpine regions clearly solve serious problems of life under extreme climatic conditions, as low temperatures, strong winds, unstable soils and in the North partly 24-h of light.

Keywords Adaptation · Alpine · Arctic · Climate change · Light · Polar · Precipitation · Snow · Temperature · Wind

Characteristics of the polar and alpine biomes

The most important environmental factor to restrict plant life in polar and alpine regions, both having a short growing season, is low temperature (Billings 1973). Permafrost in the ground, normally with a shallow active layer on top in summer, is common in most polar regions. It may also occur in some alpine regions but this is less frequent. Alpine areas are found in all parts of the world, in both tropical and polar regions, in oceanic as well as in continental and often dry areas. In the mountains of the equatorial zone there is often an enormous diurnal temperature variation. It may be said to be winter every night and summer every day (Hedberg 1957). In polar regions, the monthly mean temperatures in winter may be below – 40°C (e.g. Obasi 1996; Chernov and Matveyeva 1997), even lower in some of the most continental areas, while commonly well above 0°C during summer months in areas where snow melts. Particularly because of these differences in the temperature conditions between polar and alpine regions they are often said to have greater dissimilarities than similarities (e.g. Körner 1995), although there are also several similarities (Billings 1973).

However, in both biomes few plants only can stand the harsh temperature and other extreme environmental conditions, e.g. strong wind, often found there. Normally trees are missing both in alpine and polar regions in the Northern Hemisphere, and the absence of trees is often used as a definition of these biomes. In some districts, however, of both northern Russia and North America, the melted soil top layer in summer is deep enough to foster tree growth. Then, we get a so-called Forest Tundra in areas with a thick frozen layer further down in the ground. Detailed division of the Arctic in bioclimatic/biogeographichal zones is presented by Bliss (1981) and later defined by the CAVM Team (2003), while a brief presentation of the Alpine division and the

F. E. Wielgolaski
Department of Biology, University of Oslo, 1045,
0316 Blindern, Oslo, Norway
e-mail: f.e.wielgolaski@bio.uio.no

S. R. Karlsen (✉)
NORUT IT, 6434, 9294 Tromsø, Norway
e-mail: stein-rune.karlsen@itek.norut.no

previous Arctic divisions is given in Wielgolaski (1997a).

In temperate regions the summer temperature in particular, is the limiting factor for tree growth (Dahl 1986). Generally, the tree line is higher in continental areas with large mountain massifs than in more oceanic areas at the same latitude (Fig. 1). It is found to be as high as above 4000 m elevation in tropical areas of South America and in continental Asia (Troll 1973a), while at 0 m elevation e.g. along the coast of northern Norway (e.g. Aas and Faarlund 2001; Karlsen et al. 2005). In polar regions, soil may be unstable even on relatively gentle slopes, also at low elevation, but it might also be found at high elevations in lower latitudes. Such soil movement (solifluction) easily breaks plant roots, which, therefore, normally prevents tree growth, and has been used as one criterion to define alpine belts (Troll 1973b). Strong wind under extreme environmental conditions may also stop tree growth. Near the upper tree line, groups of "krumholz" trees, particularly of *Picea abies* (Fig. 2), are well known (e.g. Wielgolaski 1997b; Kullman 1998). The outer stems protect the inner ones against the most extreme conditions, e.g. strong winds, in such a way that the inner protected ones normally are considerably taller than the border stems. Small stands of trees at the tree line often show "flagging" i.e. most the branches lacking at the wind side, except near the ground where the buds and branches are protected by snow during winter.

In alpine areas there are often strong regional variations in the amount of precipitation. The actual snow line in the tropical Puna of South America is above 6000 m elevation, mainly as a result of extreme aridity. Low precipitation and deserts are also common at high altitudes in many continental regions of Asia (Troll 1972). However, precipitation in many, normally somewhat more humid regions of the world increases with elevation, e.g. in the Rocky Mountains (Kittel et al. 2002) and in western Fennoscandia (Aune 1993; Førland 1993), and then may cause a thick cover of snow in winter. The melting of the snow shows great local variations depending on the topography, normally of greatest importance on steep mountains, but always influencing the plant growing season (e.g. Sonesson et al. 1975; Inouye and Wielgolaski 2003).

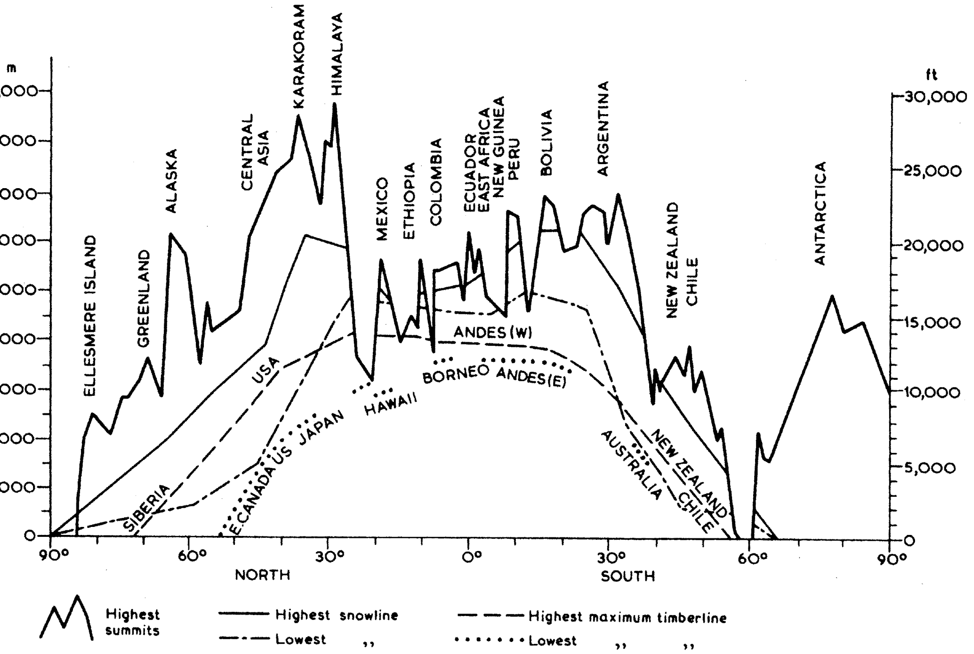

Fig. 1 Elevation in metre (and feet) of timber lines, snow lines, and highest mountain peaks on a cross-section of global alpine regions (after Swan 1967)

Fig. 2 "Krumholz " of Norway spruce (*Picea abies*) at the climatic tree line in south-eastern Norway, wind dominating from the left (west) of the picture. Most branches near the snow cover. (Photo: F.E Wielgolaski)

Often, polar regions show a low annual precipitation, commonly <100–400 mm (Bliss 1997; Chernov and Matveyeva 1997). Due to the long period of low temperature, most of it comes as snow, which further delays the length of growing season. The time for disappearance of snow cover in spring is normally the primary factor for growth start in cold regions, particularly in continental regions (Inouye and Wielgolaski 2003). However, growth may start under some snow, if the ground in more humid districts is insulated by a heavy cover and then nearly free of frost in the upper soil (Resvoll 1917; Bliss 1971; Wielgolaski et al. 2004). Due to the generally low temperatures at high latitudes also in summer, the evapotranspiration is also often low but most often approximating precipitation (Brown 1981). Therefore, wet areas are often commonly tundra, e.g. in the lowlands of polar regions (Rydén 1981).

Fig. 3 Several metre tall vegetated "Pingo", built up by an ice core in North American wetlands (Photo: F.E. Wielgolaski)

In some cases permafrost in the tundra causes part of the nearly flat areas to build up mounds with ice-cores. This is common e.g. in more continental northern Europe (palsas), but may be even more spectacular in other parts of the world as in Polar parts of North America, where conical ice-core hills may be several meters tall, the so-called "Pingos" (Fig. 3). Under such conditions the roots of plants growing on the surface easily break, which only few species will tolerate, of course.

Particularly the absence of trees both in polar and alpine biomes can very often give a similar visual impression (Wielgolaski 1986), and in both biomes there are variations from wet sedge-moss communities to dry dwarf-shrub heaths and rocky fell-fields. Solifluction, mass-flow and patterned ground, as e.g. polygons (Bliss 1997), are common both in polar communities (Fig. 4) and in high alpine or nival belts (also in the temperate region), which of course strongly influences the sparse vegetation. The broad comparability in the physiognomy of polar and alpine vegetation is clearly stressed by Barry and Ives (1974). However, they also say that the extensive wet tundra

Fig. 4 Stone-open soil polygons in a nearly flat ground in High Arctic at Spitsbergen, made by frequent ice formations in the soil, with vegetation in between. (Photo: F.E. Wielgolaski)

commonly found in the Arctic is largely lacking in alpine areas, where a complex mosaic of more mesic and xeric communities occur due to the dissected nature of the terrain.

A very important dissimilarity between polar regions and alpine regions further south is the light regime. Whereas there are possibilities for 24 h of sunshine during at least parts of the growing season in polar regions (Fig. 5), this is not the case in temperate and tropical montaneous regions. This often causes different ecotypes or provenances to develop at various altitudes and latitudes (Mooney and Billings 1961). It is also an important factor to find the best fitted cultivar of agricultural species for various districts of polar regions.

Adaptation

Plants in polar region as well as in alpine tundra are adapted by very rapid growth to the normally short growing season (Savile 1972; Wielgolaski 1997c). Heide (1985) stated that the more severe the environment, the more important survival adaptations seemed to be, while biological competition tended to be less important to the vegetation. Some tundra plant species will under extreme environmental conditions require several years to finish their life cycle, while only one season under better conditions (e.g. Sørensen 1941). A typical example of such adaptation is found in species of the genus *Salix*. Dahl (1986) stresses that in prostrate tundra species within the genus (*S. herbacea, S. polaris* and *S. reticulata*) it may take four growing seasons for development of catkins, while in taller lowland species it normally takes only one year.

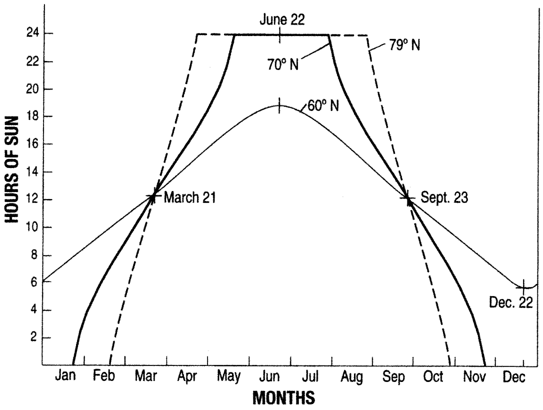

Fig. 5 Day length at various latitudes from 60°N northwards. Note the 24 h day for about 4 months in summer at 79°N (e.g. at Spitsbergen), and a similar period with sun always below the horizon in winter

Transplantation of trees originating in a temperate lowland area to a subarctic-subalpine region or between extreme environments of different types (e.g. from a subalpine temperate region to a high latitude area with 24 h daylight in parts of the growing season) has been carried out in many years. Often this has shown strong influence in productivity and phenology of the trees (Hagem 1931; Kalela 1938; Beuker 1994; Wielgolaski and Inouye 2003; Ovaska et al. 2005). Planting trees of a southern origin (provenance or ecotype) in the north, often means that the trees continue their growth late in summer and autumn in their new growth place as they are adapted normally to do on their southern district of origin. This again may cause the trees to have a weak hardening of their new shoots before an early start of low temperature and winter in the more extreme environment. Often that leads to frost damage of the buds during winter or the new shoots in spring.

If a southern provenance is transplanted to northern latitude regions with 24 h daylight during mid summer, that may also lead to growth problems due to plant physiological responses by the changes in spectral composition of the light. The plants originating from northern latitudes are for instance normally adapted to a low red to far red ratio particularly at the end of an Arctic summer (Nilsen 1986) compared to more southern provenances. This may be one factor to induce growth cessation of woody plants adapted to northern latitudes, and is also found to influence the shoot elongation (Håbjørg 1972a, b; 1978). However, temperature variations e.g. day and night may also induce senescence (Marchand et al. 2004), and is therefore important in the plant adaptation by a continued climate change (see next section).

Normally, the well hardened buds of coniferous trees (Beuker 1994) and leaf buds of mountain birch (Ovaska et al. 2005) from the northernmost ecotypes have an earlier break in spring than buds from trees of a more southern ecotype. Many agricultural plants are found to be adapted to use fewer days between various growth and flowering stages when grown in long days (Skjelvåg 1998). As temperature normally decreases to the north, this also means that many specific cultivars of agricultural plants can be grown further north than otherwise would have been possible.

The phenological transplant studies referred to above clearly indicate that the latitude, i.e. the light regime, is of strong importance for development of plants in polar regions. Adaptation to the growing condition at the place of origin in a species is also clearly stated by studies in controlled climate (e.g. in *Betula* by Myking 1999). Plants originally growing in districts with mild and unstable winters (as in the south and along the coast) showed later bud burst, particularly after only a short period of chilling (November) than more northern and inland ecotypes with cold and stable winters (Fig. 6). Differences in the date of bud burst of mountain birch originating from different elevations but approximately the same latitude, indicate that also adaptation to certain temperature regimes is of importance for start of the growing season (Ovaska et al. 2005), which is as expected.

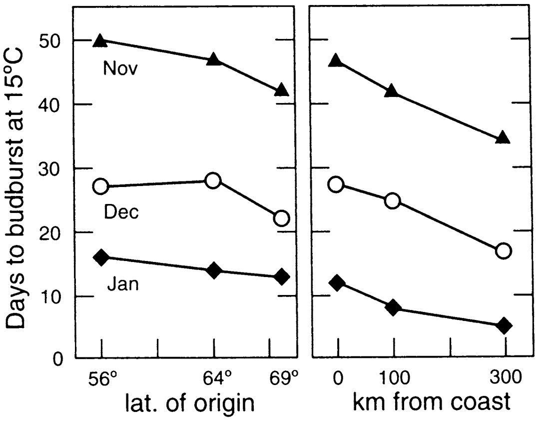

Fig. 6 Days to bud burst at 15°C in a short-day period (8 h), after different periods of chilling at 5°C, in three *Betula pubescens* ecotypes along two gradients, in **a** (left) from three different latitudes of origin and in **b** originating from various distances from the coast (reprinted from Myking 1999)

The normally very rapid growth found in plants of a short growing season, demands an adaptation to a rapid and good supply in spring of both energy and nutrients from winter storage organs (Wielgolaski 1984). The storage organs of polar and alpine plants are commonly situated belowground, close to the growing points, which normally are just above, but also at the ground itself, chamaephytes and hemicryptophytes according to the life form classification by Raunkiaer (1934), plant types dominating in these extreme climatic conditions (Table 1). That is a good adaptation to a short translocation distance to and from the buds where the stored material is used for growth in the short and very active growing season. Particularly in monocotyledons of wet sedge communities but also in forbs of mesic low alpine and low Arctic tundra, the storage organs are mainly found in the roots (Mooney and Billings 1960), resulting in a higher proportion of root mass compared to shoot mass than in most other plant communities even in tundra regions (Table 2).

In some species of tundra forbs, sedges and grasses parts of the leaves even stay green during winter to speed up growth start in spring (but then sometimes they die in early summer) (Wielgolaski 1997c). In evergreen dwarf shrubs, however, there is a late bud break and a slow translocation rate but in these species generally having a low nutrient level (Wielgolaski et al. 1975), the life form is probably more an adaptation to grow on nutrient-poor soil than a direct adaptation to live in climatic extreme conditions.

Generally, shrubs are close to their limit of survival in tundra. The plants have to be creeping to be protected by a snow cover against the lowest temperatures and the strongest wind. Close to the permanent snow cover of alpine regions and in the High Arctic the conditions are too extreme for formation of above-ground reserves in buds and woody above-ground parts, and even dwarf-shrubs are missing in these regions. Dahl (1986), however, stressed that the hardiest plants are pulvinate chamaephytes with buds just above the soil. There, the close neighbouring between several, densely tufted leaves makes the cushion to exchange heat more like a single organ of the size of the total cushion. It is normally important for

Table 1 Number of vascular plant species and percentage of different life forms, based on the classification by Raunkiaer (1934), at various alpine altitudes in southern Norway

Altitudinal limit (m)	Number of species	Life form						
		Phanerophyte (%)	Chamaephyte (%)	Hemicrytophyte (%)	Geophyte (%)	Helophyte (%)	Hydrophyte (%)	Therophyte (%)
> 2000	29		44.8	55.2				
1800–1999	39		25.6	66.7	2.6	2.6		2.6
1600–1799	75	8.0	32.0	48.0	4.0	5.3		2.7
1400–1599	63	4.8	9.5	65.1	11.1	1.6	3.2	4.8
1200–1399	138	6.5	10.1	51.4	10.1	10.1	2.9	8.7
1000–1199	109	2.8	5.5	55.0	10.1	11.9	5.5	9.2

Table 2 Different average ratios between plant parts of some tundra vegetation types (based on Wielgolaski et al. 2001)

Region	Root/shoot (live)	Non-green/green live: vascular plants	Dead/live above-ground: vascular plants
Desert and semi-desert	0.9	2.3	1.9
Wet sedge meadows	21	23	1.6
Mesic dry meadows	5.0	7.7	0.8
Dwarf-shrub tundra	3.1	12	0.6
Low shrub tundra	2.0	19	0.2
Forest tundra	0.8	15	0.1

the polar and alpine plants to absorb as much heat of the incoming radiation as possible via the soil close to the plants or by the plants themselves. This is also reflected by the plant types found and their morphological adaptations.

Very often tundra plants are covered by hairs to protect against cooling wind and evapotranspiration, and in this way also directly absorb heat for the hairy organs. They may be relatively dark in colour as often in *Draba* spp. and *Erigeron* spp. and the early emerging sepals of some polar/alpine *Ranunculus (R. glacialis, R. nivalis, R. sulphurous)*. In other plants the hairs are light coloured, silky or woolly, and light-transparent to the dark and heat-absorbing organs inside the hairs or bracts, as e.g. in cotton-grass, *Eriophorum* spp. (Dahl 1986). In some willows (*Salix* spp.), Krog (1955) observed a 15–25°C higher temperature in the catkins than in the ambient air. In these willows solar radiation penetrates the silky hairs of the dark catkin scales, which are heated also because of lower outward heat transport due to the hairs, a really effective adaptation to life in extreme environments.

It is also observed that both the orientation of many plant leaves and flowers in polar/alpine regions may be adaptations to the environmental conditions of the biomes. The leaves e.g. of many cushion plants at high altitudes (even at lower latitudes) often have a nearly vertical position to get the best reflection of incoming light to hit other leaves instead of being reflected back to the atmosphere (Dahl 1986). Better known is probably the parabolic form of many tundra flowers, which increases the absorbed radiation by reflection to the centre of the flower (Kevan 1975; Wielgolaski 1987). This is favourable to increase the temperature for pollination of the flowers and for development of the ovary. This adaptation seems to be most common in plants with a high reflection coefficient for incoming radiation by having light coloured flowers e.g. white or yellow (for instance in *Dryas* spp., Fig. 7, *Papaver* spp. and *Ranunculus* spp.). Often the flowers also change their direction during the day always to be open towards the sun (Kevan 1975; Wielgolaski 1997c). Sometimes also the colour of the flowers are adapted to change to be darker in colour after

Fig. 7 Parabolic flowers of near white colour as *Dryas octopetala* collect maximum of incoming heat to the ovary in the centre of the flower. (Photo: F.E. Wielgolaski)

pollination by insects, which are attracted by white colours, to absorb even more heat, e.g. *Ranunculus glacialis*.

Climate change

Plants living in the extreme environments of polar and alpine biomes are thus adapted to the conditions there in many ways, but growth is always modified, as in other climatic zones of the world, by the nutrient availability. Although, normally temperature is the dominant factor for growth in cold regions, light is of course also very important, particularly at increasing latitude and at the end of the growing season (see e.g. references in Arft et al. 1999). There will always be changes in the climate during a period. Generally, it is estimated that for the Northern Hemisphere annual temperature during the last 150 years has increased by 0.055° per decade (Overpeck et al. 1997; Jones and Moberg 2003). Both in northern and southern Norway Klaveness and Wielgolaski (1996) have observed earlier first flowering of most plant species in the mid 20th century than about 100 years earlier. However, warming has accelerated in recent decades in the Northern Hemisphere (IPCC 2001; ACIA 2004), which is of extreme importance for plant growth particularly in polar and alpine regions, especially if it continues also in the future. Most important is the increase in temperature but also in precipitation, both calculated to be stronger during winter than summer and in models predicted to be strongest in northern latitudes (Dickinson 1986; Maxwell 1997; ACIA 2004; Schwartz et al. 2006). In Europe the positive phase of North Atlantic Oscillation (NAO) has increased clearly in the period February–April during the last decades, leading to prevailing westerly winds and, therefore, higher temperatures and a more humid climate, particularly since the end of 1980s (Post and Stenseth 1999; Chmielewski and Rötzer 2001; Wanner et al. 2001). In northern Norway it is observed that *Cornus suecica* avoiding the most continental districts recently has been common more to the east, indicating a more humid climate there than before (Tømmervik et al. 2004). In high latitudes and altitudes of the Northern Hemisphere the recent climate change has caused higher winter precipitation as snow. Anyhow, in most lowland areas, and particularly in coastal regions, the increased temperature has caused earlier snowmelt (Maxwell 1992), the growing season to be longer (e.g. Bliss and Matveyeva 1992) and the plant population rates to be higher (Carlsson and Callaghan 1994). In extreme cold climates, however, as at the highest elevations and in the continental parts of northernmost Europe, winter temperatures have not increased enough through the last decades of the 1900s to foster earlier snowmelt. However, by continued increase of the winter temperature during the coming years, it is expected that this will change (Shutova et al. 2005; 2006).

In autumn, on the other hand, it may be speculated that somewhat lower global radiation by more cloudy weather and then also partly slightly decreasing temperatures, will continue the earlier end of the growing season calculated for parts of the more continental northernmost Europe by satellite images during the last two decades of 1900 as well as by 40 years of field phenological studies of birch leaf yellowing at Kola Peninsula (Shutova et al. 2005; 2006). The day length has been found to be important for the time of end of growing season, particularly at extreme high latitudes. Håbjørg (1972a, b) found in controlled climate (phytotron) studies that plants from northern latitudes were stronger dependent in cessation of growth by reduction in light than more southern provenances. He concluded that this might be an adaptation in the northern provenances to the markedly lowered red to far red ratio at the end of the Arctic summer.

Low autumn temperatures and then particularly low minimum values have for a long time also been suggested to be triggering yellowing and senescence of plants (Galakhoff 1938). In the International Tundra Experiments (ITEX), the temperature of intact ecosystems in the field have been manipulated at 13 circumarctic and alpine sites by using transparent open top chambers through several years. The plants within these 1–3°C warmer chambers, generally, showed somewhat later senescence than outside, but significantly only at one alpine site (Arft et al. 1999). This is in contrast to a significantly earlier start of the growing season (Henry and Molau 1997) and also of flowering at all sites by the warming. However, Marchand et al. (2004) found in experiments at Northeast Greenland, that plants heated in the field during the growing season with infrared radiation by about 2.5°C, showed a higher maximum percentage of vascular plant cover and a delay in yellowing in the autumn by approximately 15 days (Fig. 8) compared to the surrounding vegetation in NDVI analyses. They concluded that also in High Arctic tundra, higher temperatures postpone the senescence process. This may cause longer growing seasons if temperatures increases in the future. On the other hand, many plant species may be less matured for the winter, and also less fitted for the Polar light regime.

In a paper summarising the ITEX results (Walker et al. 2006), it is stressed that plant diversity is reduced within the open top chambers. However, the height and cover of deciduous shrubs and monocotyledons have increased during the experimental period, while the cover of mosses and lichens has been decreasing (Fig. 9). The changes are stronger in the Low than in the High Arctic, maybe as an indication of less nutrients being released by increased temperature at the coldest sites. It is suggested in several papers (e.g. Shaver et al. 2000) that if "soil organic matter turnover is increased due to warming, there is a high potential for redistribution of nitrogen from soils to vegetation". This results in higher production at least for a certain period.

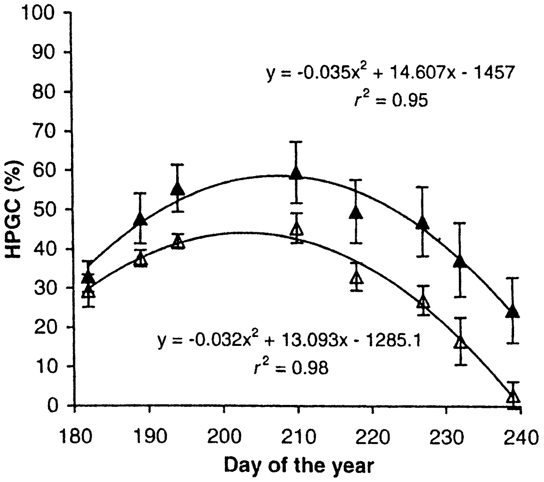

Fig. 8 Percentage higher-plant cover at unheated (lower curve) and heated in the field with infrared radiation (upper curve) at Northeast Greenland. Note that senescence is clearly delayed in the heated vegetation as studied in NDVI analyses (Marchand et al. 2004)

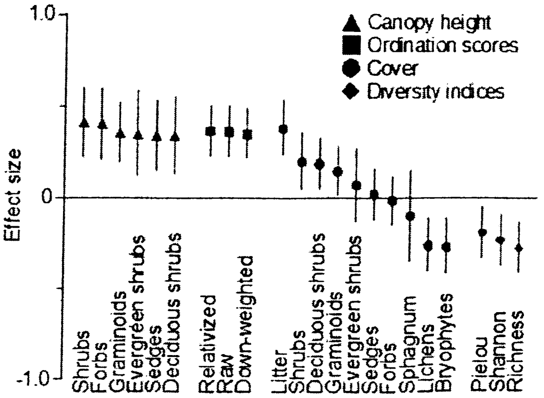

Fig. 9 Response in several tundra plant forms on heating in the field by keeping the vegetation within open top transparent chambers. Mean of results from several ITEX sites in the response on various community variables, as e.g. on the species composition (ordination scores) (Walker et al. 2006)

Near the tree line in Fennoscandia this is observed in the field particularly in mountain birch growth (own unpubl. obs.). It is also obvious that the tree line in the region has increased by 100–150 m since the mid 1980s as a result of higher temperatures (e.g. Kullman 2002), but for e.g. *Betula pubescens* ssp. *tortuosa* in Fennoscandia also by reduced browsing by livestock. The same author (Kullman 1998) has also found that trees increasing their growth after earlier temperature rises (e.g. in the 1920–1930s) at the tree line locally died in the tops when there came a decrease in winter temperature again afterwards.

The reduced cover of lichens in the ITEX-experiments was found to be significant after 3 years, while the increased cover of vascular plants was significant only after 4–6 years of warming (Walker et al. 2006). The reduction in lichen cover may be seen as a result of competition with increasing biomass of vascular plants (Cornellisen et al. 2001) or of snow melt and refreezing several times during the winter season. Such conditions will cause an ice cover influencing the O_2/CO_2 conditions for the lichens under the ice. In transplant studies of vegetation mats in an alpine region from a nearly snow free lichen heath to a near by *Vaccinium myrtillus* snow bed, one of the authors (Wielgolaski 2001) found that already after 1 year the lichen *Cetraria nivalis* had changed colour to yellow-brown, and after 4 years nearly all arbuscular lichens were dead, probably because of lack of oxygen under the ice cover. Lichen death due to climate change will be a serious problem for the survival of reindeers in many northern areas, where lichens are the main diet, particularly during winter. However, overgrazing during the last decades also has caused a dramatic decline of lichen cover in parts of northernmost Norway (Johansen and Karlsen 2005).

Remote sensing has the potential to monitor and give evidence of the ongoing climate change in Arctic vegetation at a variety of spatial and temporal scales (e.g. Stow et al. 2004). It can for instance identify changes in the above-ground production, structure and cover, in the phenological cycle, and changes in ecotone boundaries. NOAA Advanced Very High Radiometer (AVHRR) imagery is particularly valuable for land cover studies at decadal time scales since these data are available from the early 1980s to the present. Studies based on the Normalised Difference Vegetation Index (NDVI) from the AVHRR instrument have found an extensive greening trend at higher northern latitudes (e.g. Myneni et al. 1997; Bogaert et al. 2002). In arctic tundra and boreal forest there is a close relationship between temperature and NDVI (e.g. Suzuki et al. 2001; Karlsen et al. 2006; Walker et al. 2003), and the increased greenness is associated with increased air-temperature (Buermann et al. 2003; Gong and Ho 2003; Walker et al. 2003). However, the greening trend shows large regional differences. Generally, in the 1990s the North American greening trend was higher than the Eurasian trend (Slayback et al. 2003). Locally, a trend of slightly shorter length of the growing season for the period 1982 to 1998 was found in the most continental parts of northern Fennoscandia and Kola Peninsula in northwestern Russia (Høgda et al. 2001) (Fig. 10), mostly as a result of later onset of spring. A trend of changes in the short Arctic growing season length over decadal time scales is of key interest, since it could be the first indication of a shift in the above-ground production and cover. The time-integrated NDVI during the growing season is associated with the above-ground plant biomass (e.g. Walker et al. 2003). Increased time-integrated NDVI is found in northern Alaska the last decades (Jia et al. 2003; Stow et al. 2003), and the greenness increases most rapidly in areas of moist non-acidic tundra (Jia et al. 2003).

The ongoing climate change with strongly increasing temperatures particularly in the North of the Northern Hemisphere may according to

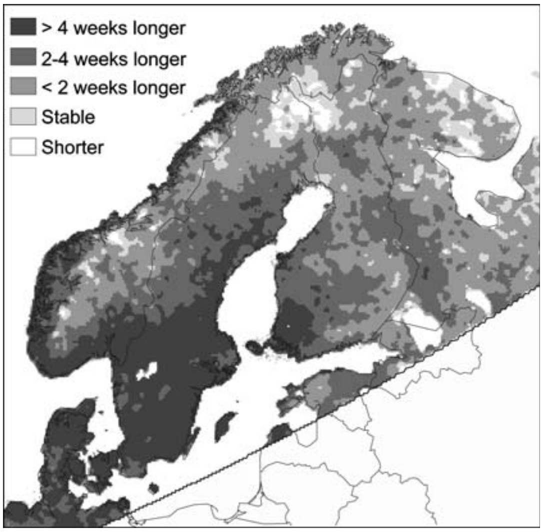

Fig. 10 Changes in length of the growing season in northernmost Europe during the period 1982–1998 as analysed by the GIMMS-NDVI satellite dataset (reprinted from Høgda et al. 2001 with permission from NORUT IT)

modelling scenarios cause a 40% reduction of the current tundra by an expected temperature increase of 4–7°C over the next 100 years (ACIA 2004). In many ways, this may cause less extreme environments for plants with replacement of the tundra by trees. However, many of these plants will not be adapted to grow in 24 h daylight. Such an adaptation takes many years, and in the meantime many of the invading plant species to the North probably will suffer seriously.

Concluding remarks

The examples given here clearly demonstrate the serious problems of life for many plants growing in Polar and Alpine Regions under extreme climatic conditions, but other problems may also occur. Low temperatures both during winter and often also summer strongly limit the diversity of plant species. Also high wind speed (Fig. 11) and unstable soil are important for many species. Both extremely low and high precipitation is observed, often in combination with temperature changes. In polar regions also the light regime is special. Having 24 h of light during parts of the growing season clearly causes a need for adaptation in plants to such conditions, both for growth, development and survival. In a changing climate with an expected much higher temperature, many of the plant species will not be mature by the end of the growing season and will die back or freeze to death during winter.

Fig. 11 Mountain birch exposed to strong wind mainly coming from the left (west) of the picture. Note also the much darker upper parts of the tree stems. That is due to growth mainly above the general snow line in winter by in particular the foliose dark brown lichen *Parmelia olivacea* (Sonesson 2001). It can be hypothesised that ice cover on snow covered trunks is one reason for lack of this lichen by reducing the O_2 availability as suggested earlier in the paper for fruticose lichens in snow beds (Photo: F.E. Wielgolaski, from a coastal mountain in Norway)

References

Aas B, Faarlund T (2001) The holocene history of the nordic mountain birch belt. In: Wielgolaski FE (ed) Nordic mountain birch ecosystems. UNESCO, Paris and The Parthenon Publ. Group, New York, London, pp 5–22

ACIA (2004) Impacts of a warming arctic. Arctic climate impact assessment. Cambridge University Press, Cambridge, UK

Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jónsdóttir IS, Laine K, Lévesque E, Marion GM, Molau U, Mølgaard P, Nordenhäll U, Raszivin V, Robinson CH, Starr G, Stenström M, Totland Ø, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. Ecol Monogr 69:491–511

Aune B (1993) Climate (Engl. Summ. pp 56–61). Nasjonalatlas for Norge. Statens Kartverk. Hønefoss, Norway

Barry RG, Ives JD (1974) Introduction. In: Ives JD, Barry RG (eds) Arctic and alpine environments. Methuen & Co Ltd., London, pp 1–13

Beuker E (1994) Adaptation to climatic changes of the timing of bud burst in populations of *Pinus sylvestris* L. and *Picea abies* (L.) karst. Tree Physiol 14:961–970

Billings WD (1973) Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. Bioscience 23:697–704

Bliss LC (1971) Arctic and alpine life cycles. Ann Rev Ecol Syst 2:405–438

Bliss LC (1981) North American and Scandinavian tundras and polar deserts. In: Bliss LC, Heal OW, Moore JJ (eds) Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge, London, New York, Sydney, pp 8–34

Bliss LC (1997) Arctic ecosystems of North America. In: Wielgolaski FE (ed) Polar and alpine tundra. Ecosystems of the world, vol. 3. Elsevier, Amsterdam, New York, Oxford, Tokyo, pp 551–683

Bliss LC, Matveyeva NV (1992) Circumpolar arctic vegetation. In: Chapin III FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic ecosystems in a changing climate. Academic Press, New York, pp 59–89

Bogaert J, Zhou L, Tucker CJ, Myneni RB, Ceulemans R (2002) Evidence for a persistent and extensive greening trend in Eurasia inferred from satellite vegetation index data. J Geophys Res 107(D11), doi:10.1029/2001JD001075

Brown J (1981) Introduction. In: Bliss LC, Heal OW, Moore JJ (eds) Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge, London, New York, Sydney, p 79

Buermann W, Anderson B, Tucker CJ, Dickinson RE, Lucht W, Potter CS, Myneni RB (2003) Interannual covariability in northern hemisphere air temperatures and greenness associated with El Niño-southern oscillation and the arctic oscillation. J Geophys Res 108(D13):4396, doi:10.1029/2002JD002630,2003

CAVM Team (2003) Circumpolar arctic vegetation map scale 1:7,500000. Conservation of arctic flora and fauna (CAFF) Map No. 1. US Fish and Wildlife Service, Anchorage, Alaska

Carlsson BA, Callaghan TV (1994) Impact of climatic change factors on the clonal sedge *Carex bigelowii*: implication for population growth and spread. Ecography 17:321–330

Chernov YI, Matveyeva NV (1997) Arctic ecosystems in Russia. In: Wielgolaski FE (ed) Polar and alpine tundra. Ecosystems of the world, vol. 3. Elsevier, Amsterdam, New York, Oxford, Tokyo, pp 361–507

Chmielewski F-M, Rötzer (2001) Response of tree phenology to climate change across Europe. Agr For Meteorol 108:101–112

Cornelissen JH, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Gwynn Jones D, Jonasson S, Chapin III FS, Molau U, Neill C, Lee JA, Melillo JM, Sveinbjörnsson B, Aerts R (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? J Ecol 89:984–994

Dahl E (1986) Zonation in arctic and alpine tundra and fellfield ecobiomes. In: Bliss LC, Heal OW, Moore JJ (eds) Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge, London, New York, Sydney, pp 35–62

Dickinson R (1986) The climate system and modelling of future climate. In: Bolin B, Doos B, Jager J, Warrick RA (eds) The greenhouse effect, climate change and ecosystems. Wiley, Chichester, UK, pp 207–270

Førland E (1993) Annual precipitation. Det Norske Meteorologiske Institutt, Kartblad (Map) 3.1.1. Nasjonalatlas for Norge. Statens Kartverk. Hønefoss, Norway

Galakhoff NN (1938) The autumnal hue and shedding of foliage (in Russ.). Bot J USSR 23:193–208

Gong D-Y, Ho C-H (2003) Detection of large-scale climate signals in spring vegetation index (normalized difference vegetation index) over the northern hemisphere. J Geophys Res 108(D16):4498, doi: 10.1029/2002JD002300

Håbjørg A (1972a) Effects of photoperiod and temperature on growth and development of three latitudinal and three altitudinal populations of *Betula pubescens* Ehrh. Meld N Landbr Høgsk 51(2):1–27

Håbjørg A (1972b) Effects of light quality, light intensty and night temperature on growth and development of three latitudinal populations of *Betula pubescens* Ehrh. Meld N Landbr Høgsk 51(26):1–17

Håbjørg A (1978) Photoperiodic Ecotypes in Scandinavian Trees and Shrubs. Meld N Landbr Høgsk 57(33):1–20

Hagem O (1931) Forsøk med vestamerikanske treslag (in Norw., German summ.). Medd Vestl Forstl Forsk 12:1–217

Hedberg O (1957) Afro-alpine vascular plants: a taxonomic revision. Symb Bot Upsal 15:1–411

Heide OM (1985) Physiological aspects of climatic adaptation in plants with special references to high-latitude environments. In: Kaurin A, Juntila O, Nilsen J (eds) Plant production in the North. Norw. Univ. Press, Tromsø, Norway, pp 1–22

Henry GHR, Molau U (1997) Tundra plants and climate change: the international tundra experiment (ITEX). Global Change Biol 3(Suppl. 1):1–9

Høgda KA, Karlsen SR, Solheim I (2001) Climatic change impact on growing season in Fennoscandia studied by a time series of NOAA AVHRR NDVI data. Proceedings IGARSS 2001 (ISBN 0–7803–7536-X) (pp 1–3). Sydney, Australia

Inouye DW, Wielgolaski FE (2003) High altitude climates. In: Schwartz MD (ed) Phenology: an integrative environmental science. Kluwer Acad. Publ., Dordrecht, Boston, London, pp 195–214

IPCC (Intergovernmental Panel on Climate Change) (2001) Summary for policymakers, third assessment report. In: Watson RT, the Core Writing Team (eds) Synthesis report. Cambridge Univ. Press, Cambridge, London, New York, Sydney, pp 1–34

Jia GJ, Epstein HE, Walker DA (2003) Greening of arctic Alaska, 1981–2001. Geophys Res Lett 30(20):2067, doi:10.1029/2003GL018268

Johansen B, Karlsen SR (2005) Monitoring vegetation changes on Finnmarksvidda, Northern Norway, using Landsat MSS and Landsat TM/ETM+ satellite images. Phytocoenologia 35:969–984

Jones PD, Moberg A (2003) Hemispheric and large-scale surface air temperature variations: an extensive revision and an update to 2001. J Clim 16:206–223

Kalela A (1938) Zur Synthese der experimentellen Untersuchungen über Klimarassen der Holzarten. Comm Inst For Fenn 26:1–445

Karlsen SR, Elvebakk A, Johansen B (2005) A vegetation-based method to map climatic variation in the arctic-boreal transition area of Finnmark, north-easternmost Norway. J Biogeogr 32:1161–1186

Karlsen SR, Elvebakk A, Høgda KA, Johansen B (2006) Satellite based mapping of the growing season and bioclimatic zones in Fennoscandia. Global Ecol Biogeogr 15:416–430

Kevan PG (1975) Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. Science 189:723–726

Kittel TGF, Thornton PE, Royle JA, Chase TN (2002) Climates of the rocky mountains: historical and future patterns. In: Baron J, Fagre D, Hauer R (eds) Rocky

Mountain Futures: An Ecological Perspective. Island Press, Covelo, California, pp 59–82

Klaveness D, Wielgolaski FE (1996) Plant phenology in Norway—a summary of past and present first flowering dates (FFDs) with emphasis on conditions within three different areas. Phenol Season 1:47–61

Körner C (1995) Alpine plant diversity: a global survey and functional interpretations. In: Chapin III FS, Körner C (eds) Arctic and alpine biodiversity. Springer-Verlag, Berlin, Heidelberg, pp 45–62

Krog J (1955) Notes on temperature measurements indicative on special organization in arctic and subarctic plants for utilization of radiated heat from the sun. Phys Plant 8:836–839

Kullman L (1998) Tree-limits and Montane forests in the Swedish scandes: sensitive biomonitors of climate change and variability. Ambio 27:312–321

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish scandes. J Ecol 90:68–77

Marchand FF, Nijs I, Heuer M, Mertens S, Kockelbergh F, Pontailler J-Y, Impens I, Beyens L (2004) Climate warming postpones senescence in high arctic tundra. Arctic Antarctic Alp Res 36:390–394

Maxwell B (1992) Arctic climate: potential for change under global warming. In: Chapin III FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic ecosystems in a changing climate. Academic Press, New York, pp 11–34

Maxwell B (1997) Recent climate patterns in the arctic. In: Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, Sveinbjörnsson B (eds) Global change and arctic terrestrial ecosystems. Springer-Verlag, New York, pp 21–46

Mooney HA, Billings WD (1960) The annual carbohydrate cycle of alpine plants as related to growth. Am J Bot 47:594–598

Mooney HA, Billings WD (1961) Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna*. Ecol Monogr 31:1–29

Myking T (1999) Winter dormancy release and budburst in *Betula pendula* ROTH and *B. pubescens* EHRH. Ecotypes Phyton (Austria) 39:139–145

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386:698–702

Nilsen J (1986) Plantenes reaksjon på daglengde og spektral energifordeling (in Norw.). Ottar: 30–38

Obasi GOP (1996) Climatological normals (Clino) for the period 1961–1990. WMO/OMM-No 847

Ovaska JA, Nilsen J, Wielgolaski FE, Kauhanen H, Partanen R, Neuvonen S, Kapari L, Skre O, Laine K (2005) Phenology and performance of mountain birch provenances in transplant gardens: latitudinal, altitudinal and oceanity–continentality gradients. In: Wielgolaski FE (ed) Plant ecology, herbivory, and human impact in nordic mountain birch forests. Springer-Verlag, Berlin, Heidelberg, New York, pp 99–115

Overpeck J, Hughen K, Hardy D, Bradley R, Case R, Douglas M, Finney B, Gajewski K, Jacoby G, Jennings A, Lamoureux S, Lasca A, MacDonald G, Moore J, Retelle M, Smith S, Wolfe A, Zielenski G (1997) Arctic environmental change of the last four centuries. Science 278:1251–1256

Post E, Stenseth NC (1999) Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339

Raunkiaer C (1934) The life forms of plants and statistical plant geography. Clarendon Press, Oxford

Resvoll TR (1917) Om Planter som Passer til Kort og Kold Sommer (in Norw.). Archiv for Matematik og Naturvidenskab 35:1–224

Rydén BE (1981) Hydrology of Northern tundra. In: Bliss LC, Heal OW, Moore JJ (eds) Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge, London, New York, Sydney, pp 115–137

Savile DBO (1972) Arctic adaptations in plants. Can Dept Agric Monogr 6:1–81

Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the northern hemisphere. Global Change Biol 12:343–331

Shaver GR, Canadell J, Chapin FS III, Gurevitch J, Harte J, Henry G, Ineson P, Jonasson S, Melillo J, Pitelka L, Rustad L (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. BioSci 50:871–882

Shutova E, Wielgolaski FE, Karlsen SR, Makarova O, Haraldsson E, Aspholm PE, Berlina N, Filimonova T, Flø, L, Høgda KA (2005) Phenology of nordic mountain birch in relation to climate change at Kola Peninsula and the trans-boundary pasvik-enare region. Proceedings of the 17th international congress of biometeorology ICB September 2005, Garmisch-Partenkirchen, Germany. Deutscher Wetterdienst, Annal Meteorol 41(2):524–527

Shutova E, Wielgolaski FE, Karlsen SR, Makarova O, Berlina N, Filimonova T, Haraldsson E, Aspholm PE, Flø L, Høgda KA (2006) Growing seasons in nordic mountain birch in northernmost Europe as indicated by long-term field studies and analyses of satellite images. Int J Biometeorol DOI: 10.1007/s 00484-006-0042-y

Skjelvåg AO (1998) Climatic conditions for crop production in nordic countries. Agr Food Sci Finl 7:149–160

Slayback DA, Pinzon JE, Los SO, Tucker CJ (2003) Northern hemisphere photosynthetic trends 1982–99. Global Change Biol 9:1–15

Sørensen T (1941) Temperature relations and phenology of northeast greenland flowering plants. Medd Grønl 125:1–305

Sonesson M (2001) Ecology of some epiphytic lichens on the mountain birch. In: Wielgolaski FE (ed) Nordic mountain birch ecosystems. UNESCO, Paris and The Parthenon Publ. Group, New York, London, pp 63–70

Sonesson M, Wielgolaski FE, Kallio P (1975) Description of Fennoscandian tundra ecosystems. In: Wielgolaski FE (ed) Fennoscandian tundra ecosystems, part 1 plants and microorganisms. Springer-Verlag, Berlin, Heidelberg, New York, pp 3–28

Stow DA, Daeschner S, Hope A, Douglas D, Petersen A, Myneni R, Zhou L, Oechel W (2003) Variability of the seasonally integrated normalized difference vegetation index across the north slope of Alaska in the 1990s. Int J Rem Sens 24:1111–1117

Stow DA, Hope A, McGuire D, Verbyla D, Gamon J, Huemmrich F, Houston S, Racine C, Sturm M, Tape K, Hinzman L, Yoshikawa K, Tweedie C, Noyle B, Silapaswan C, Douglas D, Griffith B, Jia G, Epstein H, Walker D, Daeschner S, Petersen A, Zhou L, Myneni R (2004) Remote sensing of vegetation and land-cover change in arctic tundra ecosystems. Rem Sens Environ 89:281–308

Suzuki R, Nomaki T, Yasunari T (2001) Spatial distribution and its seasonality of satellite-derived vegetation iindex (NDVI) and climate in Siberia. Int J Climat 21:1321–1335

Swan LW (1967) Alpine and aeolian regions of the world. In: Wright HE Jr, Osbura WS Jr (eds) Arctic and alpine environments. Indiana Univ. Press, Bloomington, pp 29–54

Tømmervik H, Johansen B, Tombre I, Thannheiser D, Høgda KA, Gaare E, Wielgolaski FE (2004) Vegetation changes in the nordic mountain birch forests: the influence of grazing and climate change. Arctic Antarctic Alpine Res 36:323–332

Troll C (1972) Geoecology and the world-wide differentiation of high-mountain ecosystems. In: Troll C (ed) Geoecology of the high-mountain regions of Eurasia. Franz Steiner Verlag, Wiesbaden, pp 1–13

Troll C (1973a) The upper timberlines in different climatic zones. Arctic Alp Res A3–A18

Troll C (1973b) High mountain belts between the polar caps and the equator: their definition and lower limit. Arctic Alp Res A19–A27

Walker DA, Epstein HE, Jia GJ, Balser A, Copass C, Edwards EJ, Gould WA, Hollingsworth J, Knudson J, Maier HA, Moody A, Raynolds MK (2003) Phytomass, LAI, and NDVI in northern Alaska: relationship to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar arctic. J Geophys Res 108(D2):8169, doi: 10.1029/2001JD000986

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jónsdóttir IS, Klein JA, Magnússon B, Molau U, Oberbauer SF, Reva SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland Ø, Turner PL, Tweedie CE, Webber PJ, Wookey PA (2006) Plant community responses to experimental warming across the tundra biome. PNAS 103:1342–1346

Wanner H, Brönnimann S, Casty C, Gyalistras D, Luterbacher J, Schmutz C, Stephenson DB, Xoplaki E (2001) North Atlantic oscillation–concepts and studies. Surv Geophys 22:321–382

Wielgolaski FE (1984) Functioning of tundra vegetation in relation to life forms. In: Margaris NS, Arianoustou-Farragitaki M, Oechel WC (eds) Being alive on land. Dr W Junk Publ., The Hague, pp 13–19

Wielgolaski FE (1986) Production-ecology and functioning of polar and alpine ecosystems. In: Polunin N (ed) Ecosystem theory and application. John Wiley & Sons, Chichester, pp 12–34

Wielgolaski FE (1987) Floral processes. In: Nelson JG, Needham R, Norton L (eds) Arctic heritage. IUCN, Ottawa, pp 80–94

Wielgolaski FE (1997a) Introduction. In: Wielgolaski FE (ed) Polar and alpine tundra. Ecosystems of the world, vol. 3. Elsevier, Amsterdam, New York, Oxford, Tokyo, pp 1–5

Wielgolaski FE (1997b) Fennoscandian tundra. In: Wielgolaski FE (ed) Polar and alpine tundra. Ecosystems of the world, vol. 3, Elsevier, Amsterdam, New York, Oxford, Tokyo, pp 27–83

Wielgolaski FE (1997c) Adadaptation in plants. In: Wielgolaski FE (ed) Polar and alpine tundra. Ecosystems of the world, vol. 3, Elsevier, Amsterdam, New York, Oxford, Tokyo, pp 7–10

Wielgolaski FE (2001) Field-and bottom layer vegetation mat transplantation: a method to simulate possible effects of climate change? Skogræktarritid Iceland 2001:167–170

Wielgolaski FE, Kjelvik S, Kallio P (1975) Mineral content of tundra and forest tundra plants in Fennoscandia. In: Wielgolaski FE (ed) Fennoscandian tundra ecosystems, part 1 plants and microorganisms. Springer-Verlag, Berlin, Heidelberg, New York, pp 316–332

Wielgolaski FE, Bliss LC, Svoboda J, Doyle G (2001) Primary production of tundra. In: Bliss LC, Heal OW, Moore JJ (eds) Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge, London, New York, Sydney, pp 187–225

Wielgolaski FE, Inouye DW (2003) High Latitude Climates. In: Schwartz MD (ed) Phenology: an integrative environmental science. Kluwer Acad. Publ., Dordrecht, Boston, London, pp 175–194

Wielgolaski FE, Karlsen SR, Høgda KA (2004) Plant phenology in Norway related to climate change and latitude. In: van Vliet AJH (ed) Proceedings of the international conference “Challenging Times”, April 2003. Wageningen, The Netherlands, pp 96–102