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Effects of climate change on terrestrial ecosystems

Report from a seminar in Trondheim 16.01.1990

Edited by
Jarle I. Holten

NINA

NORSK INSTITUTT FOR NATURFORSKNING

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Abstract

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A new Norwegian climate scenario predicts a temperature increase of about 2 °C for the summer months and 3-4 °C for the winter months, under doubled atmospheric CO_2. The new climate will influence several physiological processes in plants, like photosynthesis and respiration. Higher agricultural production is predicted. However, limited possibilities for genetic adaptation for forest trees and slow migration will lead to a retreat of Norway Spruce northeastwards in northern and Central Europe. The frost-sensitive Beech and Oak will expand their areas northwards and northeastwards in Europe. Rapid climatic change will disturb the phenological cycle of many plants. The southern regions of Scandinavia may experience an increase in plant diversity, whereas there will be a decrease in plant diversity in the mountains. The existence of many high mountain plants is threatened. Frostsensitive, thermophilous and weedy species will expand. A large number of retarding factors will probably result in only small changes in the flora and vegetation during the next 50 years. The changes will mainly be quantitative in most districts of North Europe. In Central Norway a new temperate zone and a more thermic oceanic section will allow invasion of strictly Central European and southwest European species. Extreme climatic events may enhance certain developments, for instance catastrophic death of forests caused by drought or frost.

Key words: Climatic change, primary production, genetic adaptation, plant diversity, vegetation zones, migration barriers.

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Referat

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Et nytt norsk klima-scenario forutsier en temperaturøkning på ca 2 °C for sommermånedene og 3-4 °C for vinter-månedene, ved fordoblet CO_2 -innhold i atmosfæren. Det nye klimaet vil påvirke mange fysiologiske prosesser i planter, slik som fotosyntese og respirasjon. Det forutsies høyere jordbruksproduksjon. Begrensede muligheter til genetisk tilpasing (lang levetid) for skogstrær, og lav spredningshastighet vil føre til en retrett nordøstover i Nord- og Sentral-Europa for bartrær som gran og furu. Frostømfintlige arter, f.eks. bøk, vil ekspandere nordover og østover i Europa. Raske klimaendringer vil forstyrre den fenologiske syklusen hos mange planter. Sørlige deler av Skandinavia vil få økt plantediversitet, mens fjellområdene vil få lavere plantediversitet. Eksistensen til en del fjellplanter er truet. Et stort antall forsinkende faktorer vil sannsynligvis føre til bare små forandringer i flora og vegetasjon de neste 50 årene. Forandringene vil i hovedsak være kvantitative i de fleste deler av Nord-Europa. I Midt-Norge vil en ny temperert vegetasjonssone og en mer termisk oseanisk seksjon tillate invasjon av sterkt varmekjære og frostømfintlige arter fra Mellom- og Sydvest-Europa. Ekstreme klima-episoder vil forsterke visse utviklingstendenser, f.eks. katastrofe-død av skogstrær forårsaket av tørke eller frost.

Emneord: Klimaendringer, primærproduksjon, genetisk tilpasning, plante-diversitet, vegetasjonssoner, vandringsbarrierer.

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Preface

A seminar including 7 invited lecturers from Norway, Sweden and the Netherlands, was held 16 January 1990 at the Museum of Science and Archaeology, University of Trondheim. The seminar topic was "ecological effects of climatic change". The seminar was arranged by the Norwegian Institute for Nature Research, Trondheim, and funded by the Norwegian Ministry of the Environment. In addition to the last lecture, chapters 4 and 5 have been written by the editor.

Trondheim Oktober 1990
Jarle Inge Holten

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1 Climate scenarios

Climate change in Norway due to increased greenhouse effect

Arne Grammeltvedt
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A group of scientists (Eliassen et al. 1989) has evaluated available results from global climate models (GCM) with the aim of preparing various scenarios for future climate changes in Norway. Due to uncertainties in the results of GCMs, in particular on the regional level, only one scenario has been specified. In this scenario an increase in greenhouse gases corresponding to a doubling of CO_2 in the atmosphere is assumed. Based on present trends of greenhouse gases, this is likely to occur around the year 2030.

New results are expected to become available in autumn 1990 through the WMO/UNEP Intergovernmental Panel on Climate Change. The scenario developed for Norway will be re-evaluated in the light of these new results.

Quantitative results obtained by GCMs are at present uncertain. The treatment of feedback mechanisms, in particular changes in cloud cover, and the coupling between the atmosphere and the ocean, are the main sources of uncertainty.

Most of the GCMs predict a global increase in average surface temperature by between 2 and 4 °C. The models with the most realistic description of heat exchange between air and sea, and of heat transport by ocean currents predict a global temperature increase of 2 °C. Only a few of the GCMs have a spatial resolution which allows analysis of predicted climate changes in Norway. Important local effects are not included in the models.

The currently most likely climate changes to result from a change in the greenhouse effect on the atmosphere corresponding to a doubling of the CO_2 concentration are as given below. Statements marked ^{xx} are considered to be "almost certain", those marked ^{x} are "more uncertain".

Temperature - globally

^{xx} The temperature of the lower stratosphere will decrease.

^{xx} The temperature of the lower troposphere and at ground level will increase. The annual average global mean temperature is expected to rise by about 2 °C.

^{x} The increase of the annual average surface temperature will be largest at high latitudes and smallest in the tropics.

^{x} At high latitudes, the temperature increase will be most pronounced during autumn and winter.

Temperature - Norway

^{x} The average winter (December, January, February) temperature will increase by 3-4 °C. The north-south gradient of this increase is expected to be small. The increase will be smaller in coastal areas compared to inland areas.

^{x} The average summer (June, July, August) temperature will increase by about 2 °C.

Precipitation/Hydrology - globally

^{xx} The water cycle will be intensified.

^{x} At high latitudes, precipitation amounts will increase during all seasons. Soil moisture will increase during winter.

Precipitation/Hydrology - Norway

^{x} Precipitation will increase in all seasons, but most pronouncedly during spring.

^{x} Showers will bring a larger fraction of the precipitation.

^{x} Soil moisture will increase during winter, decrease during summer.

Variability - Norway

The present cyclone (low pressure) activity is not expected to change significantly.

Sea level. The sea level rise will be 15-20 cm. This will be caused by thermal expansion of the ocean. Melting of inland ice is not expected to contribute significantly.

Literature

Eliassen, A., Grammeltvedt, A., Mork, M., Pedersen, K., Weber, J.E., Braathen, G. & Dovland, H. 1989. Climate change in Norway due to increased greenhouse effect. Report to the Ministry of the Environment. - Unpubl.

2 Ecosystem processes and primary production

Probable effects of climatic change due to the greenhouse effect on plant productivity and survival in North Europe

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Introduction. A scenario has been constructed by the geophysicists on the probable climate of North Europe with a carbon dioxide content of the atmosphere double the present level of 330 ppm. Due to the greenhouse effect summer temperatures are expected to be about 2 degrees C higher than now, while winter temperatures are expected to be 4 degrees C higher than at present. Incidentally, this is not very different from the climatic conditions in Scandinavia during the thermal maximum after the last ice age. At that time, trees grew up to about 300 m higher in relation to present topography than today, corresponding to a temperature difference in summer of about 2 degrees C. Heat-demanding plants like the misteltoe (*Viscum album*) had a wider distribution than today, suggesting a similar change (Skre 1979). Pollen of holly (*Ilex aquifolium*), which is a frost-sensitive plant, has been found in bogs near Hamar, whereas today it is found not much nearer than Arendal on the south coast or around Gothenburg. This suggests a difference in winter temperatures of more than 4 degrees C, perhaps 6 degrees.

In this contribution I shall try to estimate expected changes in plant productivity potential and distribution of crops and wild plants due to the heating of the atmosphere. This is based on results of research on the ecological geography of plants during the last decades in Norway.

Greenhouse effect on agricultural production in Norway. The basis of plant production is photosynthesis whereby energy from the sun is trapped by the plants and transformed to chemical energy which is used in production of organic matter. The amount of organic matter produced is termed the gross primary production. However, plants like other living beings must respire to live, and this consumes some of the material produced. What is left is termed the net primary production which is the contribution of the vegetation to the ecosystem. All animals, including man, depend on this production.

For photosynthesis, solar energy and carbon dioxide are necessary. The carbon dioxide is taken up through the stomata. However, the cells under the stomata are wet. Hence, as carbon dioxide diffuses inwards through the stomata, a loss of water by transpiration is unavoidable. Water is taken up by the plant roots and used in transpiration. If the water uptake is less than transpiration the plant looses water. If this reaches a certain point the plants close their stomata and the water loss is thereby reduced. But at the same time the uptake of carbon dioxide also stops and thus also photosynthesis. Hence, a supply of water is necessary for photosynthesis.

But even if water and solar energy are available, there will be little or no production under cold conditions, something we see in winter. Temperature must be sufficiently high to permit necessary physiological processes to go on with sufficient speed. Hence, plant temperature can also be a factor limiting production.

These are the basic climatic factors limiting plant production and all will be affected by the greenhouse effect. I shall try to assess the changes, their magnitude and direction.

Besides the climatic effects of the increased CO_2 content of the atmosphere there may be a direct effect on plant productivity (Eamus & Jarvis 1989). Numerous laboratory experiments show increased assimilation as a response to increased concentration of CO_2 in the atmosphere. This is used commercially in greenhouse cultures by increasing the content of CO_2 in the air to increase productivity. However, such experience cannot uncritically be applied to what might happen in natural ecosystems. Positive effects might not appear if other factors limit production, such as available light, available water or sufficiently high temperatures. Plants adapt in various ways to increased carbon dioxide concentration in the environment, and this must be examined in long-lasting experiments.

Light limitation for photosynthesis. Light absorbed in the chlorophyll provides by photosynthesis the energy needed to reduce carbon dioxide to carbohydrates or equivalent organic compounds. The carbon dioxide is attached to an acceptor, in C-3 plants ribulosebiphosphate (RuBP), in C-4 plants phospho-enol-pyruvate (PEP). The energy of 8 light quanta absorbed in the chlorophyll is needed to reduce a molecule of carbon dioxide. But in the process the acceptor is used up and must be regenerated. This also requires an additional 4-5 quanta of light energy so that the total becomes 12-13 quanta for each molecule of CO_2 fixed (Farquhar & v. Caemmerer 1982, Raven 1983). In this respect there is little difference between C-3 and C-4 plants. The average energy of 12 moles of quanta absorbed in chlorophyll (photosynthetically active radiation, PAR) compared with the combustion value of 1/6 of a mole of glucose gives an energy efficiency of the PAR of 19 %.

Only part of the solar radiation is photosynthetically active, about 45 %. Thus, the maximum efficiency of the total solar radiation becomes 8.5 %

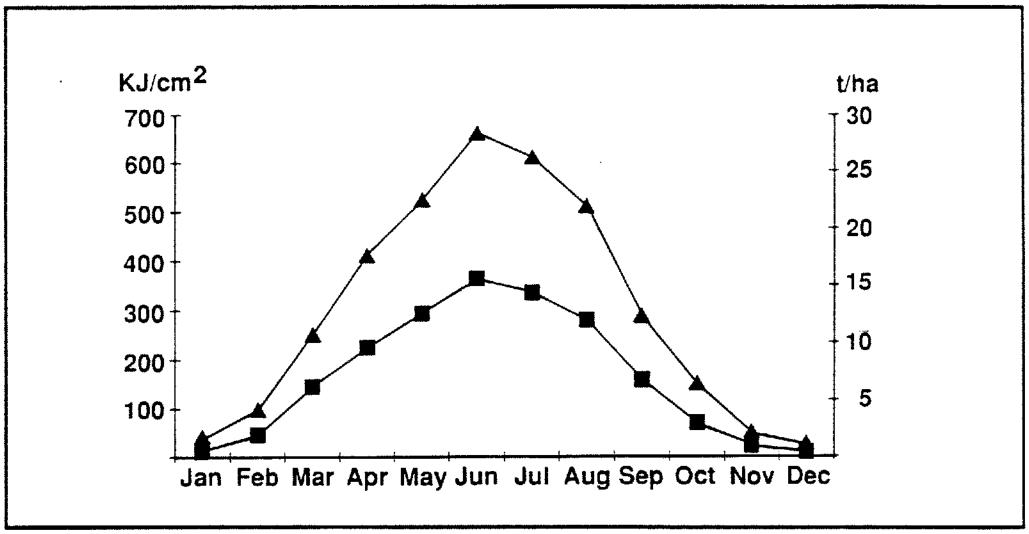
But even this cannot be attained. This is energy absorbed in the chlorophyll. But some radiation is absorbed in other organs than leaves, some is reflected and some is attenuated to a level where the plants can no longer use it for production. In crops well provided with water and fully developed foliage this loss is assessed to 20 %. Thus the maximum efficiency is now 6.8 %.

This is maximum gross primary production. But plants must, like all living organisms, respire to provide energy for the growth processes. From what will be explained later this respiratory loss is hardly lower than 20 %. Thus, maximum net primary production limited by light is 5.5 %.

Even this is too high because some respiration is needed for maintenance and transport. Comparing this with available data on primary production, peak productions of 4-5 % have been attained both in C-3 and C-4 crops (Loomis & Gerlakis 1975) which is not much below the maximum possible. An efficiency of 2-3 % is obtainable and 1 % is common for plant production during the growth season in agriculture. Other factors than light also limit agricultural production, e.g. availability of CO_2 .

Figure 1 gives the average incoming radiation at Ås near Oslo for each month, based on the period 1966-1975. I have also added a curve for net primary production based on an efficiency of 4 %. It will be

Figure 1 Incoming solar energy (KJ/cm^2/month, triangles) and maximum plant production (t/ha, squares) in 1966-1975 at Ås, SE Norway, assuming that 4 % of the solar energy is converted to dry matter.



seen that light is so low in the winter months that a higher temperature in winter will contribute little to an increased plant production, and might have negative effects due to increased respiration.

Water as a limiting factor for agricultural production. For photosynthesis, carbon dioxide must be transported from the atmosphere to the chloroplasts through the stomata. As CO_2 diffuses inwards through the stomata a loss of water by diffusion in the opposite direction, i.e. transpiration, is unavoidable. If the supply of water is lower than the transpiration, the stomata close; but then uptake of CO_2 is prevented.

When CO_2 is transported from the atmosphere to the chloroplasts there are a series of resistances. There is a resistance from free atmosphere to the vicinity of the leaves, a boundary layer resistance from the surrounding air to the openings of the stomata, a stomatal resistance by the transport through the stomata and finally a complex resistance from the air under the stomata to the chloroplasts which is called mesophyll resistance. We shall try to estimate the minimum number of water molecules lost per CO_2 molecule fixed under different climatic conditions.

If the concentration of CO_2 in the atmosphere is ca and the concentration of CO_2 in the air inside the stomata is ci then the flux is

(1) $Fc = (ca - ci)/rs'$

where rs' is the diffusion resistance for the transport of CO_2 from the atmosphere to the air inside the stomata.

If the concentration of water vapour in the atmosphere is ea and the concentration in the air space inside the stomata is ei then the transport of water through the stomata to the free air is

(2) $Fv = (ei - ea)/rs$

where rs is the diffusion resistance for the transport of water vapour from the substomatal cavity to free air.

The ea can be calculated from meteorological measurements. It is assumed that the air in the substomatal cavity is saturated with water. If the temperature of the leaf is known ei can be calculated. Leaf temperatures depend mainly on the radiation balance and transpiration. In agricultural crops with fully developed foliage and well supplied with water, leaf temperatures are usually close to air temperatures. If rs is known the rate of transpiration can be calculated, or inversely, if transpiration is known rs can be calculated.

There is a known relationship between rs and rs'. The CO_2 molecule is larger than the H_2O molecule and therefore moves more slowly by diffusion. The diffusion rate depends on the molecular weight. Hence,

(3) $rs' = 1.56\ rs$

By dividing equation 1 by 2 and using 3 we get

(4) $F = Fc/Fv = 0.64\ (ca - ci)/(ei - ea)$

where F is **the water use efficiency**, i.e. the number of molecules CO_2 taken up for photosynthesis in relation to the number of molecules of water lost. The only unknown factor is the ci, the carbon dioxide concentration in the substomatal cavity.

The ci depends among other things on the mesophyll resistance to CO_2 transport. This has been assessed in the following way.

We place a leaf saturated with light in a ventilated cuvette and measure carbon dioxide uptake as well as transpiration. The carbon dioxide uptake is used to estimate the sum of stomatal and mesophyll resistance. The transpiration rate is used to estimate the stomatal resistance to water vapour transport. Using eq. 3 the stomatal resistance to carbon dioxide transport is calculated. Then the mesophyll resistance to carbon dioxide uptake can be calculated.

The available measurements have been reviewed by Körner et al. (1979) who found that on average for C-3 plants the mesophyll resistance was 4.7 times the stomatal resistance, with extremes 2.9 and 6.3. For C-4 plants an average factor of 1.3 was obtained, testifying that C-4 plants are better adapted to hot and dry environments.

If a factor of 4 and a gradient from free air of 345 ppm to a fixation concentration on the acceptor on the chloroplasts of 30 ppm is assumed, one can calculate the concentration of CO_2 under the stomata to 282 ppm or a concentration difference of 63 ppm between open air and the substomatal cavity.

There is, however, another method for calculating the desired resistances by using carbon isotopes (Farquhar et al. 1982). When carbon dioxide is fixed on the acceptor C 12 is preferred to C 13, i.e. there is a discrimination against the heavy isotope C 13. Hence the ratio C 12/C 13 is different in the photosynthate than in the atmosphere. There is also a discrimination against C 13 in the diffusion of CO_2 from the atmosphere to the substomatal cavity since C 13 is heavier than C 12, but this is a very weak discrimination. If the photosynthesis is mainly limited by the mesophyll resistance there will be a strong discrimination, if the photosynthesis is mainly limited by diffusion the overall discrimination is weak. Hence the C 12/C 13 ratio can be used for these purposes, i.e. to estimate to what extent CO_2 concentration in the atmosphere limits plant production. In this way, Körner et al. (1988, Table 5 p. 630) have calculated a difference of close to 90 ppm in the CO_2 concentration between the substomatal cavity and free air at an altitude of 500 m in Austria. This is higher than the 63 estimated above. The question is, which of these is realistic?

It must be emphasized that in the growth cuvettes all other external resistances than the stomatal are minimized. But in the field there is an additional resistance from the free atmosphere to the air around the leaves and a boundary layer resistance from the surrounding air to the opening of the stomata. During the day the air surrounding the leaves is depleted in CO_2. All these factors also contribute. And since the C 12/C 13 method measures actual performance in the field, the maximum CO_2 gradient of 90 ppm is preferred.

If the carbon dioxide concentration in the atmosphere is doubled, the difference in the concentration between the air and the substomatal cavity is increased, and this increases Fc. This means that the water use efficiency is increased. This is also borne out by experimental evidence (Eamus & Jarvis 1989). Hence the plants produce more with the same amount of available water. Since summer drought is an important limiting factor in continental tracts this is expected to result in higher agricultural productivity. Since a higher precipitation in Norway is also envisaged in the climatic scenario, the importance of drought as a limiting factor for plant production in Norway is diminished.

Temperature as a limiting factor for plant production. It does not help if water and light are available but the temperature is low. This is obvious in temperate, boreal and arctic regions in winter; when the water freezes the production stops. And even at temperatures above zero the plants grow slowly in the autumn or early spring. Plant production depends on chemical processes and all such processes are slow at low temperatures. But we need a more precise model to estimate the limitations of low temperatures on plant production.

A producing plant can be thought of (Figure 2) as a factory. It has a raw materials department which utilizes solar energy, carbon dioxide, etc., and produces raw materials in the form of carbohydrates,

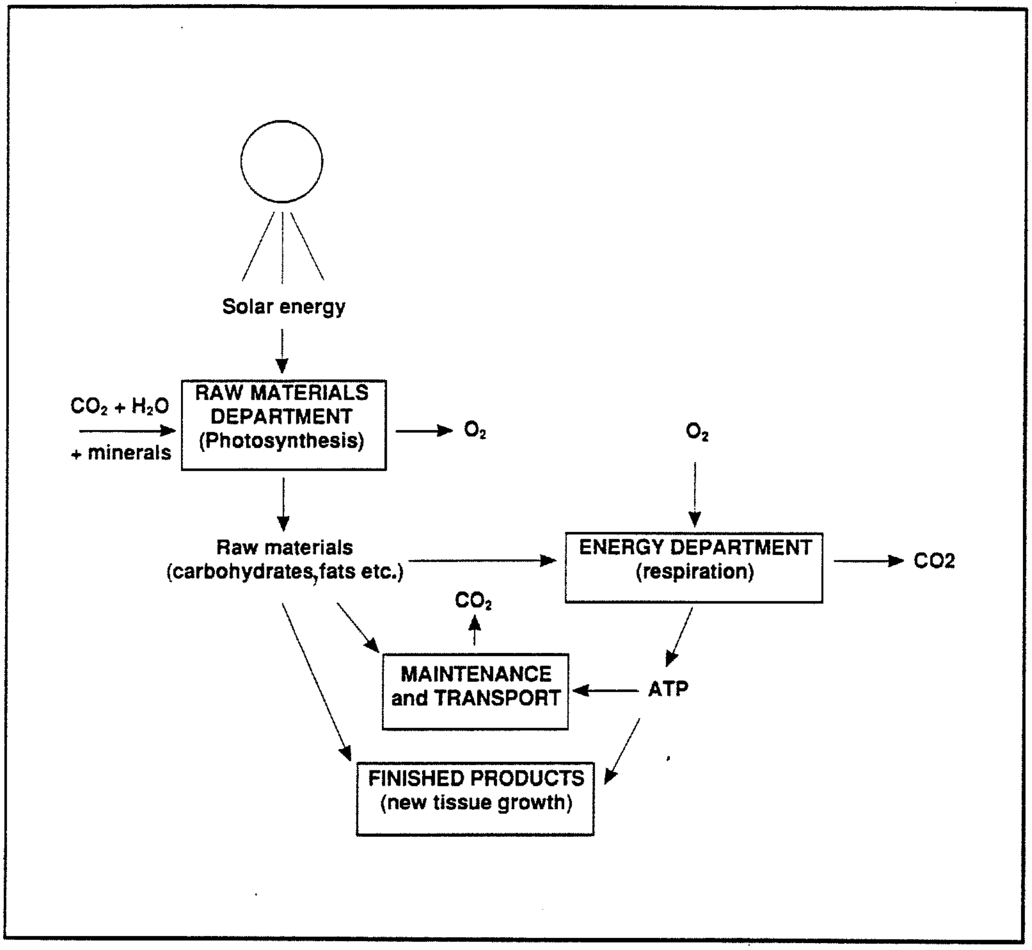


Figure 2 The plant production system (Dahl 1986). Further explanation in the text.

fats, amino acids, etc. But the raw materials must be transformed to new tissue, e.g. cellulose, proteins, etc., during the growth process, especially in the meristems. However, the chemical processes from raw materials to finished products require additional energy in the form of ATP. The ATP is produced by dark respiration in the mitochondria. We now see the dark respiration as an energy department which provides energy needed for the growth processes. Energy and raw materials are both necessary for growth. Dark respiration is strongly influenced by temperature. Our hypothesis is that at low temperatures the energy supply by respiration becomes the rate-limiting factor for growth.

We can support this by results obtained by Penning de Vries (1974, 1975, de Vries et al. 1989). Let us first take a simple physiological process in plants, the synthesis of cellulose from glucose. For the incorporation of an additional carbohydrate in the cellulose, two ATP are needed. Thus

$$n\ C_6\ H_{12}\ O_6 + 2n\ ATP = (C_6\ H_{10}\ O_5)n + n\ H_20 + 2n\ ADP + 2n\ P$$

The ATP is produced from glucose during the dark respiration and this requires more glucose than is incorporated in the cellulose. This involves an additional use of glucose of 7 %. In addition, one ATP is used up by the transport of glucose from the chloroplasts to the meristems where growth takes place.

Similar calculations can be made for different products. Proteins require much energy, about 66 %, fat 20 % and lignin 26 %. To produce an average maize plant involves a respiration loss of 20 % (Penning de Vries op. cit.). That is the figure used previously as the difference between gross and net primary productivity. In general, crops producing carbohydrates have higher yields than those producing proteins.

In a meristem of maize is supplied with carbohydrates but producing the ATP in its meristem, one new g of maize tissue cannot be produced before an equivalent of 0.2 g glucose is respired. The time it takes to respire the corresponding amount of glucose is necessarily dependent on the temperature, and the time it takes is inverse of the respiration rate. Thus the efficiency of temperature for growth is in proportion to the respiration rate at low temperatures.

Confirmation of this idea has been obtained by studying the growth of the apical shoot of spruce in a subalpine forest in Norway. Here, moisture is abundant and daily solar radiation high, but temperature is low. The daily growth of the shoot increases with increasing temperature. Temperatures were measured by means of a thermograph, and a curve of respiration as a function of temperature was obtained by the Warburg technique. Taking weights from the respiration curve the sum of the respiration values equivalent to the temperatures from the thermograph records (Re sum) was obtained and compared with growth. A very good linear correlation was obtained (Figure 3). The regression curve crosses the zero axis at a certain value; this is the amount needed for transport and maintenance (basal respiration). Only respiration in excess of that needed for transport and maintenance results in growth.

When calculating the limitations of low temperatures on plant production, temperatures must be given weights according to their effect on respiration. Fortunately, the respiration curves for different temperate plants are not very different. At low temperatures the respiration follows the Arrhenius curve with Q 10 (10 to 20 degrees C) between 2.0 and 2.8. For spruce the value is 2.7. Methods are available for calculation of Re sums for any desired combination of Q 10 and basal respiration from data published in standard meteorological records (Skre 1972). Such Re-sums correlate well with the distribution limits of plants that require high summer temperatures (Skre 1979) and with the altitude of the climatic timberline (Dahl 1986).

There is evidence that crop production, at least in temperate areas, is positively correlated with temperature. The Japanese International Biological Program analysed the results of production measurements in numerous experimental plots by means of partial regression analysis and found a positive correlation between yield and temperature down to subtropical areas. It is also well known that the growth of forests in Scandinavia, under similar conditions regarding soil fertility and availability of water, is strongly positively correlated to summer temperatures and duration of the growth season.

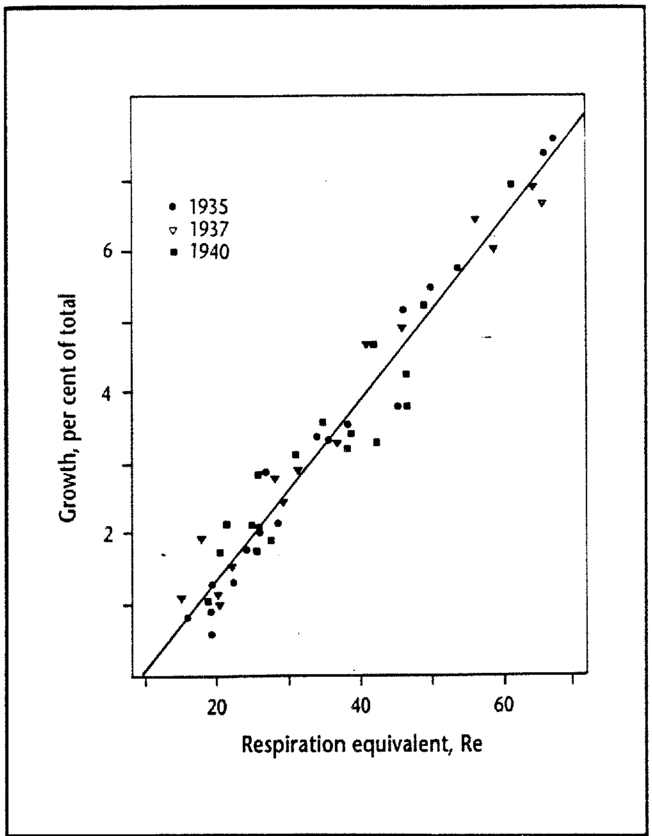


Figure 3 The relation between the daily apical growth of Norway spruce (*Picea abies*) in a subalpine forest in Norway and the sum of temperatures weighted according to their effect on respiration (Re sums) (Dahl & Mork 1959).

The greenhouse effect is expected to give us warmer summers, and especially a longer production season. Both are expected to result in higher agricultural production. Also new crops can be introduced. Today, Norway is just at the edge of maize production. If the future turns out as suggested by the scenario, probably the entire boreo-nemoral region could become an area for maize production.

Also the rather extensive areas in Norway below and above the timberline today could become important areas for the production of fodder and root crops.

But these improvements will depend upon the introduction and development of new cultivars in agriculture. The high productivity in Norwegian agriculture is to a considerable degree the result of the development of new and more productive crop cultivars; the small-grain cultivars used today produce about 30 % more grain per unit area and year than those in use 20 years ago. Different types have been developed for the different growth conditions in different parts of Norway, and different cultivars of grains are used when spring is late than in years when spring is early. Hence new cultivars of agricultural plants must be developed in response to the changed climatic conditions, but with the help of modern plant breeding methods these difficulties can be overcome. The situation is different for wild plants, including our forest trees.

The greenhouse effect and the distribution of wild plants. While agriculture has good possibilities for adapting to the new climatic conditions by developing new cultivars, the situation is different for forest trees and for many wild plants. The reason is that adaptation takes place by evolution; the genetic make-up of the populations changes as climate changes. This is a slow process taking many generations. Within a time-span of 100 years we may experience a climatic change of about the same magnitude as the change between the coldest period of the last ice age 18 000 years ago and the warmest period after the last ice age 6000 years ago. The postglacial climatic change took 12 000 years, permitting plants to adapt to the new conditions by evolving new biotypes. Now a climatic change of similar magnitude may take place in perhaps two generations of forest trees, leaving limited possibilities for genetic adaptation.

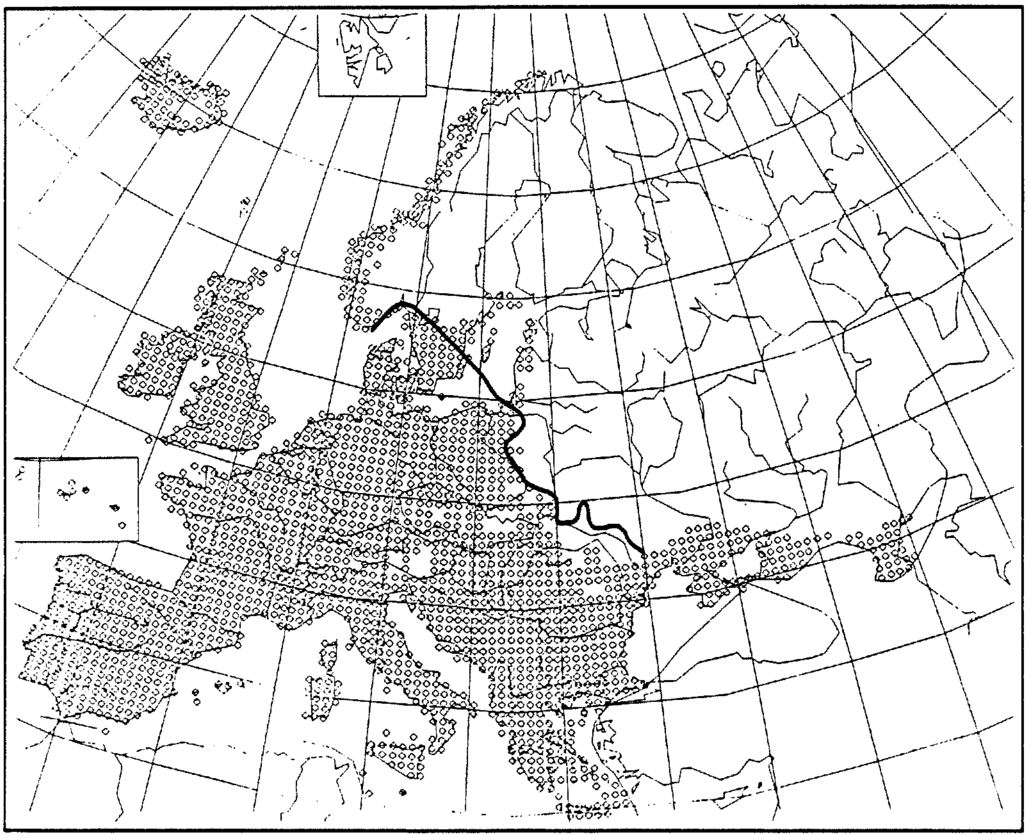
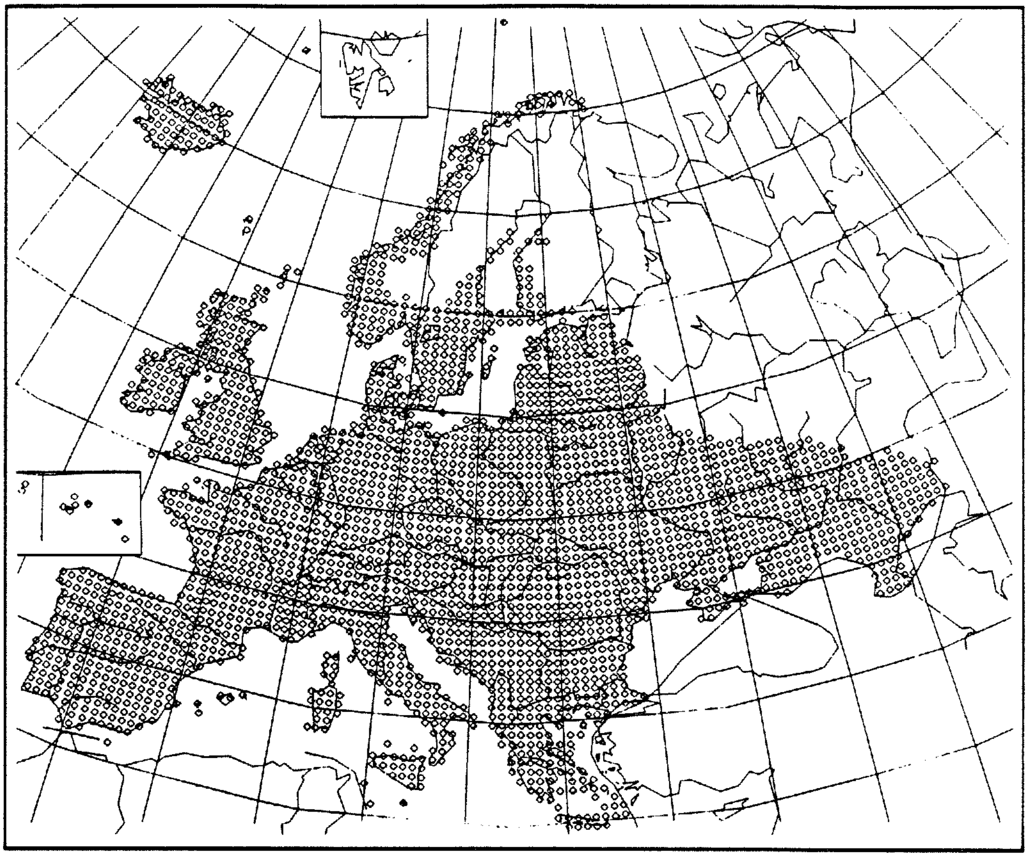


Figure 4 Distribution of beech (*Fagus sylvatica*) in relation to the –3 degrees C isotherm for the coldest month and its potential area if the distribution is limited by the –7 degrees C isotherm – see figure p. 14.



We have reasons to believe that the distribution of several forest trees is limited by climatic factors which are changing due to the greenhouse effect. An example is the distribution of beech (see Figure 4a) which is a frost-sensitive species. Its distribution limit in Europe is correlated with the -3 degrees C isotherm of the coldest month as measured at meteorological stations. Apparently it is unable to withstand frosts with temperatures under -40 degrees C, and the probability for occurrence of such severe frosts is correlated with the mean winter temperatures. Under the new climatic scenario the distribution of beech is therefore expected to correlate with the present-day -7 degrees C isotherm (Figure 4b). Thus an invasion of beech into new areas is expected. Many frost-sensitive plants with a southern and western distribution in Europe are expected to expand their distribution in response to warmer winters.

The prospect for Norway spruce (*Picea abies*), our most important forest tree, is the opposite. The spruce has a very distinct limit to the southwest in Europe (see Figure 5). In the south it is restricted to relatively high altitudes growing in the Alps mainly above 500 m, while it is found at lower levels farther north. Its southwestern distribution limit correlates well with the -2 degrees C isotherm. The underlying physiological mechanism is still obscure; in plantations it grows quite well outside its natural distribution limit. But apparently it does not reproduce well by natural means and when felled, the planted spruce stands must be replaced by new planting. Under the conditions of the climatic scenario with doubled CO_2 its natural distribution limit is expected to correlate with the -6 degrees C present-day isotherm (see Figure 6), i.e. the spruce may disappear from large lowland tracts of Northern Europe. It is also expected that the distribution of pine will be affected, although it tolerates somewhat milder winters than spruce. These trees will be replaced by deciduous trees such as beech and oak. In Norway, spruce is expected to become a montane species found at some altitude in the eastern valleys.

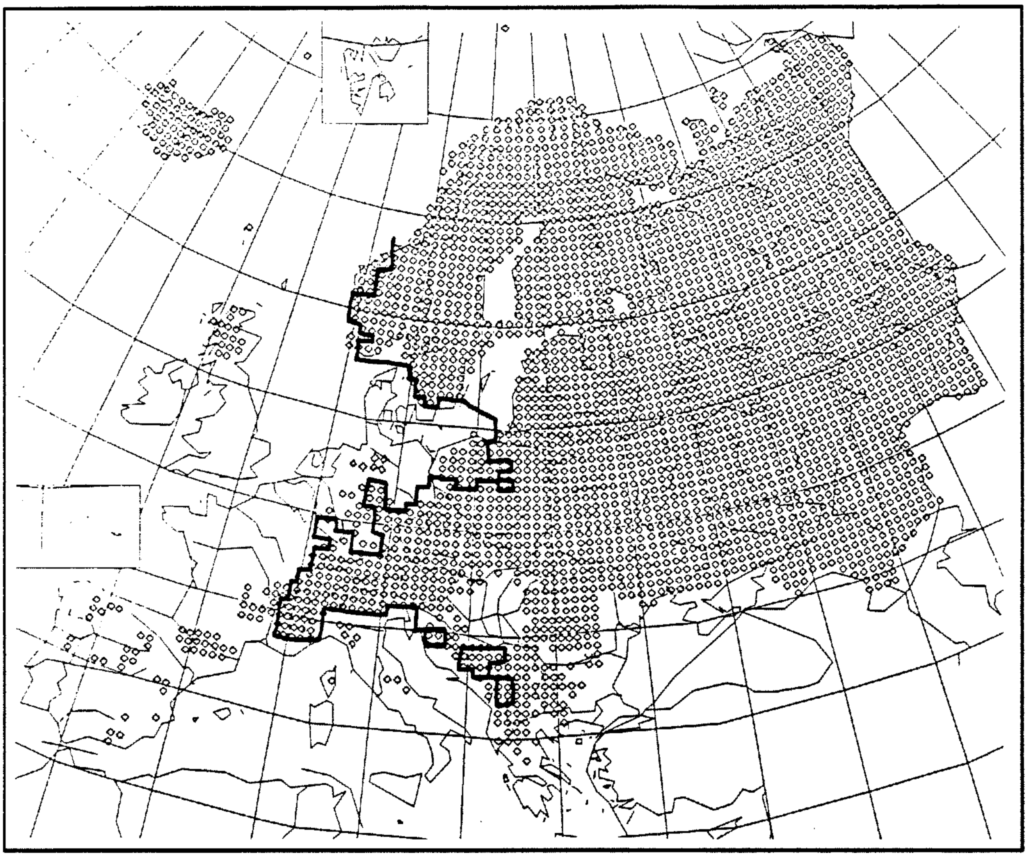


Figure 5 Distribution of Norway spruce (*Picea abies*) in relation to the -2 degrees C isotherm for the coldest month calculated for the highest points in the landscape.

There is a considerable number of other species which do not grow well in areas with mild winters. For the lack of a better term they have been called **southwest coast avoiders.** The physiological mechanisms involved are still unclear, but when such species are planted in a garden in Stavanger one often sees that they start growth during mild periods in winter and are subsequently damaged by later frost.

Quite a number of wild plants, including important forest species like oak, ash, and other deciduous trees, are limited by low summer temperatures. Such species are expected to expand in response to warmer summers. This question will be more fully explored by Mr. Skre. On the other hand, many species are restricted to areas of low summer temperatures, among them many alpine and arctic species. The distribution limits of such species are strongly correlated with maximum summer temperatures (Dahl 1951, Conolly & Dahl 1970) and some of them may be killed by overheating on hot days (Gauslaa 1984). A number of them, such as *Campanula uniflora* (Figure 7), are restricted to high altitudes on calcareous soils and may have no ecological niche left with an increase in maximum summer temperatures of 2 degrees C.

The greenhouse effect and ecotype differentiation. For a plant to survive in our North European climates it is important that its phenological cycle is coordinated with the annual climatic cycle so that it starts growing at the right time of the year, flowers and sets seeds which become ripe before winter, and that the winter buds are hardened before winter sets in. This coordination is carried out by reactions of the plants to day-length and temperature fluctuations. A very common mechanism in our flora is that short days in autumn lead to the formation of winter buds, and a period with short days and low temperatures in autumn and winter is needed for the initiation of next years' flowers. But the flowers will not develop before a period of long days in spring. The critical length of the days, the number of cycles

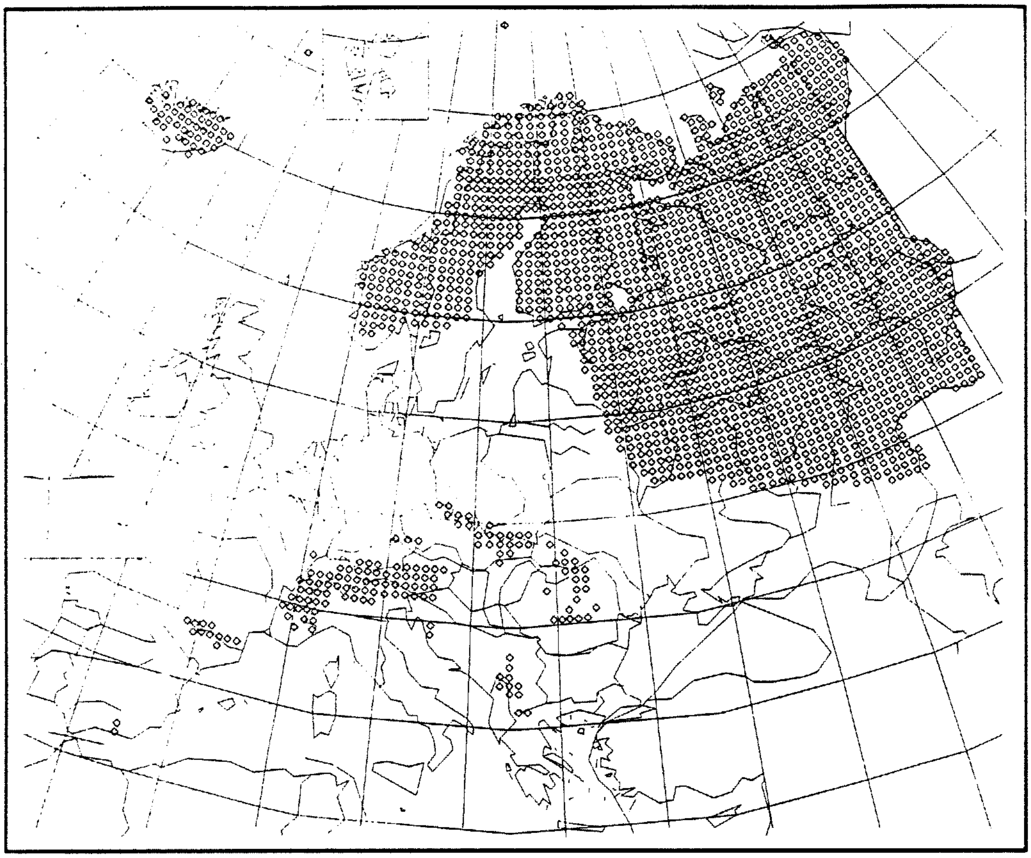


Figure 6 Potential natural distribution of Norway spruce (*Picea abies*) as limited by the -6 degrees C isotherm for the coldest month calculated for the highest points in the landscape.

needed for the reaction and the level of temperatures for the cold treatment varies between species and also between different strains in one and the same species. These parameters are clearly related to the growth conditions in the natural environment. Thus a spruce population from Central Norway stopped growth in autumn when the daylength became shorter than 21 hours, while a population fom Austria first stopped growth when the photoperiod became shorter than 15 hours (Heide 1974). A common experience is that when a northern or alpine biotype is transplanted to more southern or lowland areas it starts growth earlier in spring, but also stops growth earlier in autumn than local biotypes. Transplanted populations from south to north or from lowlands to higher levels start growth later in spring, but continue growth later in the autumn. These properties are genetically fixed. This results in a differentiation of widespread species in a number of local ecotypes, in forestry they are called **provenances**, adapted to local conditions. If climate changes, the populations have to adapt by evolving new biotypes. This is a slow process taking many generations, and if climate changes abruptly with a short time for evolution it is more likely that the local population will die out. While temperature would change, the photoperiod would remain the same and thus cause a dissociation of the temperature and photoperiod synchronization that would have a similar effect as a corresponding cross-latitudinal transfer of plants.

These features are important in forest plantations where provenances are often transplanted; if this is not done with care there are usually unfortunate results. Experience shows that transplantation of spruce provenances within one and the same district over more than 300 m in altitude is not to be recommended; for pine the altitudinal limit is 200 m (Anonymous 1961). If summer temperatures change 2 degrees C and winter temperatures 4 degrees C, this corresponds to an altitudinal difference of more than the 300 m, corresponding to the limit recommended by the Norwegian forest aut-

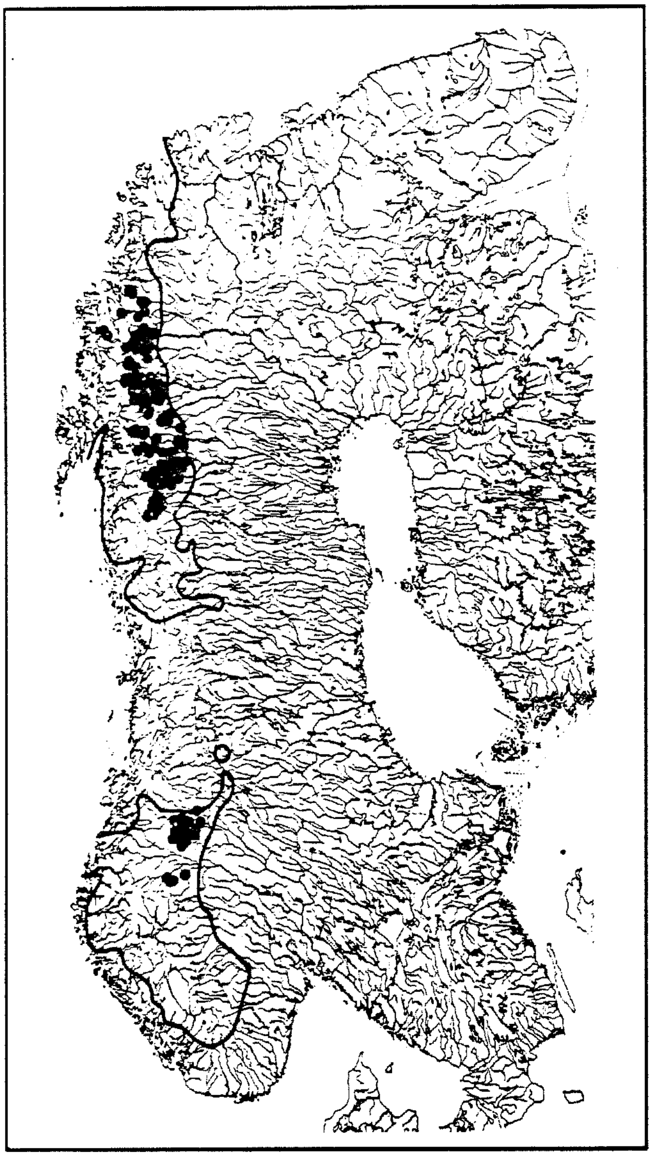


Figure 7 Distribution of *Campanula uniflora* in Fennoscandia in relation to the 22 degrees C isotherm for maximum summer temperature (Dahl 1951).

horities for planting of spruce, and more than the limit recommended for pine. One may expect previously unknown forest damage in to appear extreme years.

The situation for very many rare and threatened plants may be still more critical. Plants are usually rare because they have specialized habitat requirements. If habitat conditions change abruptly, with no time for adaptation by evolution, the chances are high that the plants will become extinct.

From the point of view of conservation, the abrupt change of climate due to the greenhouse effect must be expected to result in the disappearance of a large number of plant and animal species, and hence a loss of genetic capital. The plants and animals having the best chances of survival may be short-lived species with a large number of offspring, as we find them in pests and weeds. The more long-lived climax species will have smaller chances of survival.

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Consequences of possible climatic temperature changes for plant production and growth in alpine and subalpine areas in Fennoscandia

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Tree line formation. In alpine and arctic areas where climate is constantly changing between a cold and a warm season, most plants will have evolved different methods to survive the unfavourable season, and the selection pressure will be determined by abiotic factors rather than by competition (Kallio 1984). Plants whose winter buds, bark and needles have developed a high tolerance against freezing and drying stress will therefore have an advantage. During the year plants are subjected to many kinds of damage. To repair this and protect the living tissue against new damage, and for reproduction, growth and active uptake in roots, more energy is needed and is obtained by the production of ATP through photosynthesis and respiration (see Figure 1). Plants growing close to their distribution limits will therefore usually be restricted by demands for high temperatures to complete their life cycle and to produce viable seeds and/or winter buds (e.g. Heikinheimo 1932, Langlet 1960).

One of the most important distribution limits in Fennoscandia is the arctic and alpine tree line. The most important tree-line forming species are mountain birch (*Betula pubescens*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). According to the above-mentioned relationships, the development of flower buds (Hagem 1917) and vegetative buds (Romell 1925, Hustich 1944, Junttila & Heide 1981) in spruce and pine is mainly determined by the climate of the preceding summer. After flowering, the immature seeds start to develop embryo and storage tissue. Hagem (1917) and Heikinheimo (1921) found that the temperature during seed maturation was an important restricting factor and that embryos in the seed from tree line areas were often weak and incompletely developed. According to these authors the alpine tree lines of spruce and pine in Scandinavia are mainly seed maturation limits. In good seed-bearing years, however, viable seed may be dispersed more than 100 m above the position of their mother trees, giving rise to sterile individuals. The same relationship is also found in mountain birch (*Betula pubescens*). Mork (1944), however, found that in birch the limiting factor was not seed maturation but rather the low soil temperature that did not allow seeds to germinate, except in clear-felled areas or where the soil surface is exposed to radiation. When the seedlings are established, however, they often develop a polycormic, shrub-like, life form that is able to reproduce vegetatively (Kallio et al. 1983). According to Elkington (1968) and Vaaramo & Valanne (1973) the polycormic life form in birch may be partly a result of inbreeding by dwarf birch (*Betula nana*) in the population. Also the spruce (*Picea abies*) has a high potential for vegetative reproduction by layerings, so-called "krummholz" (Tranquillini 1979). The pine (*Pinus sylvestris*) does not have this ability, but compensates by a high seed production. Hagem (1917) found that near the tree line in southeast Norway the pine trees were often of the same age, stemming from one or a few good seed-bearing years. The mean time between these years was found to be 45 years in the Femunden area. If this time lapse happens to be too long, the old trees would eventually die out without any new seedling establishment. The same relationship should also apply to the vegetative clones of spruce and polycormic birch above the tree line. Like birch, the pine will easily reproduce from seeds in burned areas, because of its high seed production and the favourable microclimate in such areas (Kujala 1927).

Respiration as a restricting factor for growth. A plant will undergo different stages when growth is concentrated to certain organs. As a rule stem elongation takes place first, then leaf growth and the secondary radial growth in the stem. The root growth usually starts in spring but is interrupted during the period of shoot growth, and then continues into the autumn as long as the soil temperature is high enough (Hagem 1947, Rutter 1957). The growth of an organ may be divided into three stages or phases. In a leaf the dry weight increase is expressed by the growth rate (r) and time (t). As the photosynthetic and respiratory tissues are developing, growth will increase according to the following law, stated by Blackman (1919):

$$(1)\quad W = W_{oe}rt$$

where W is the dry weight at time t and W_o the initial weight. This law may be applied to the first phase, which lasts until the metabolic tissue is fully developed (West, Briggs & Kidd 1920). Then a constant growth phase will occur, followed by the third phase during which leaf growth continuously decreases and finally stops (Figure 2). This scheme may also be applied to other organs such as stems, roots, etc., and to the total leaf and shoot growth. During the second phase, growth is constant, i.e. independent of time, and its relation to external factors may be studied. In spruce shoots this phase lasts from the stage when about 20 % of the final shoot length is completed until 80 % is attained (Romell 1925, Mork 1941).

To account for the observed requirements for high temperature, various empirical parameters have been introduced (cf. Skre 1972). The most common is the **heat sum** $W = (t-t_o)$, i.e. the accumulated temperature above a certain threshold value. In the calculation of heat sums, growth is assumed to be a linear function of temperature.

The **triterm** or **tetraterm**, i.e. the mean temperature during the three og four warmest months of the year, has been widely used in forestry to express the high temperature demands for seed ripening in tree species (e.g. Hagem 1917, Kujala 1927, Mork 1933, Heikinheimo 1932, Opsahl 1952, Aas 1964). However, from the exponential shape of growth curves as a function of temperature (Went 1957) one should expect better correlation when high temperatures are given relatively more weight than low temperatures. To correct for this error Mork (1941) introduced the concept of **growth units**, based on the mean temperature during the six warmest hours a day. When using growth units instead of mean temperatures, Mork (1960) found significantly better correlation with daily apical growth in spruce, as long as water was not a limiting factor.

However, by using different combinations of variables, isolines may be constructed in a strictly empirical way following almost any limit on the map. For a satisfactory explanation of a distribution limit a good correlation as well as a physiological mechanism explaining the correlation, is needed. For the correlation between the distribution limit of coastal species like *Ilex aquifolium* and the January mean temperature the limiting factor is presumed to be frost hardiness. For the lower limits of alpine species like *Koenigia islandica* their sensitivity to extreme high temperatures has been suggested (Dahl 1951). However, no specified physiological process has yet been suggested to explain the distributions of plants restricted to areas with warm summers.

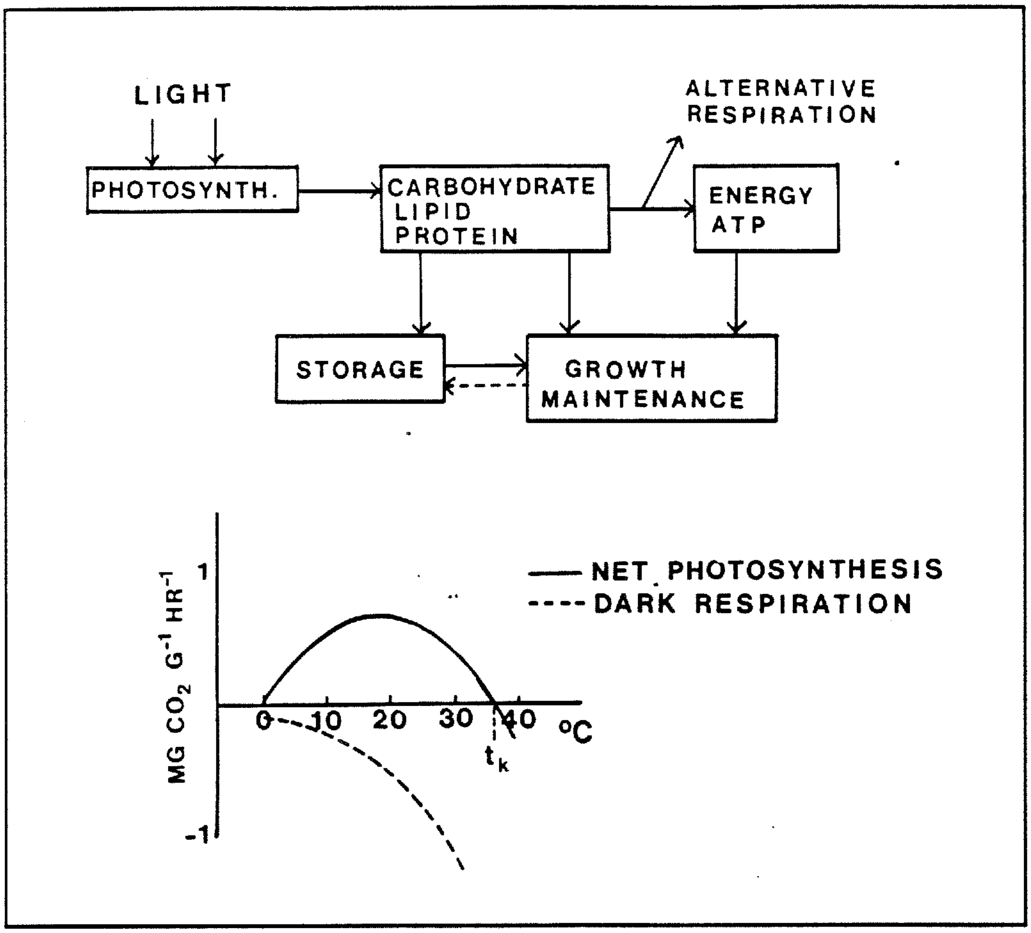


Figure 1 Diagram showing the flow of assimilates and energy in plants (top) and net photosynthesis and dark respiration rates in a subarctic moss, *Sphagnum subsecundum*, based on Skre & Oechel (1979), as a function of temperature.

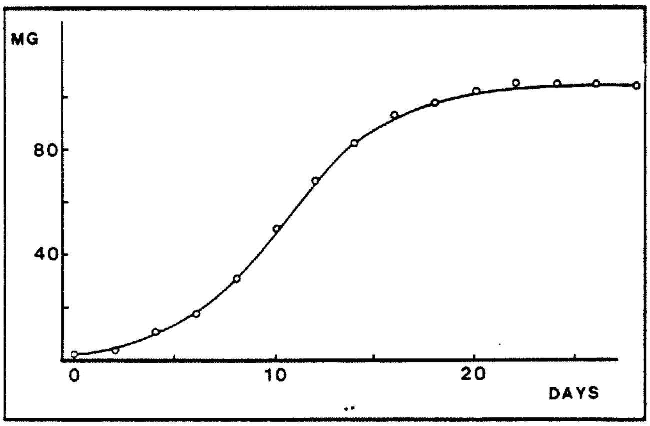


Figure 2 Growth in leaf biomass of elm (*Ulmus glabra*) in mg/leaf.

One possible mechanism for the temperature effect on plant distribution has been suggested by Dahl & Mork (1959) and Skre (1972) based on data from Norway spruce (*Picea abies*). Through photosynthesis solar energy is transformed to chemical energy and stored in different organic compounds. Differentiation and growth involve the synthesis of new plant tissue. This is an energy-consuming process depending on the supply of organic matter from photosynthesis as well as chemical energy released through the dark respiration process (Figure 1). The energy is released in small steps through the production of adenosine triphosphate (ATP) and other energy-rich compounds, which are translocated to sites where growth takes place. This part of the respiration process, which is called **growth respiration** (Penning de Vries 1972, Douce & Day 1985), is located in the mitochondria and is related to ATP production, while **the light-dependent photorespiration** (Zelitch 1966) and the alternative or **cyanide-resistant respiration** (e.g. Lambers 1980) do not involve such a formation.

Several authors have examined net photosynthesis (i.e. the difference between gross photosynthesis and photorespiration) and dark respiration in terms of gas exchange and dry-matter increase as a function of temperature, e.g. Mooney et al. (1964) on a number of alpine plants, Aalvik (1939) and Hagem (1947) on Norway spruce, Vowinckel et al. (1975) on black spruce (*Picea mariana*) and Sveinbjörnsson (1983) on mountain birch. They found that net photosynthesis increased with increasing temperatures up to a certain optimum value and then decreased (Figure 1). If plants are grown for a long time at a temperature close to their compensation temperature t_k, growth may be limited by the supply of organic matter. In the field this situation may occur during mild winters when net photosynthesis and t_k are lowered due to light limitation (cf. Printz 1933, Hagem 1947). Due to respiration loss and winter damage on evergreen needles, buds and stem tissue, plants experience a net loss of organic matter during the winter, and before new leaf tissue is formed in spring there is a further net loss of energy to produce new growth (Kozlowski & Gentile 1958). For this reason the net photosynthesis has been commonly looked upon as the limiting process for growth in a cold environment (e.g. Billings 1974, Chapin 1979, Tranquillini 1979). However, the period when net photosynthesis is negative usually lasts for only one or two months of the growing season (Rutter 1957) after which the new leaves take over as the carbon source and produce new growth that will compensate for the loss of organic matter within a short time, due to favourable light conditions. Figure 1 shows that as temperature drops below t_k there is an exponential decrease in dark respiration while net photosynthesis is still high. At low and medium temperatures above freezing point, dark respiration or growth respiration may therefore be the limiting process for growth. In this case a linear relationship between accumulated respiration and growth would be expected. Such a relationship was found by Dahl & Mork (1959) by interpreting measurements on shoot elongation in spruce from a subalpine area in southeastern Norway (Mork 1941). They found that the daily apical growth during the constant growth phase was closely correlated ($r_{xy} = 0.978$) with the daily accumulated respiration, or **respiration equivalent** (Re). The dark respiration as a function of temperature was found in separate experiments using the Warburg manometric technique. In general there is an approximately exponential increase in dark respiration as a function of temperature at low and medium temperatures (Figure 3) in accordance with Arrhenius' law (Moore 1962) for thermochemical reactions (2):

$$(2)\quad Re = ce^{-u/RT},\ \ln Re = -u/RT \ln C$$

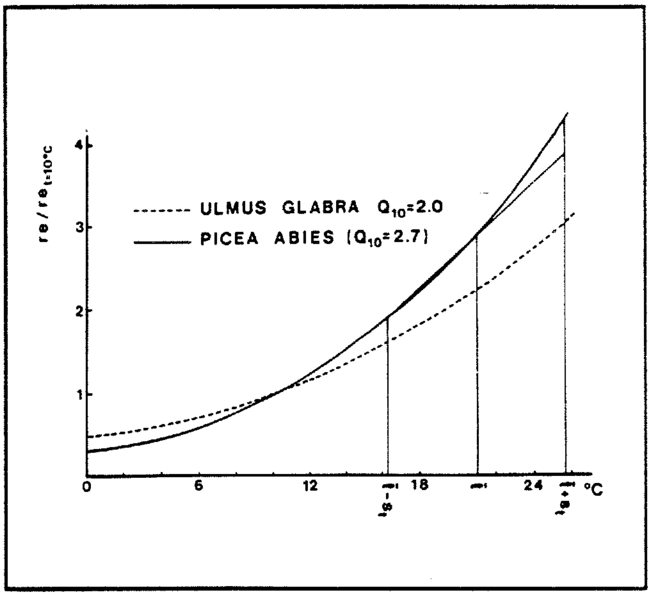


Figure 3 Dark respiration rates in growing shoots of spruce (Dahl & Mork 1959) and leaf discs of elm, measured in relative units, where the respiration at 10 °C is taken as unity. The elm leaves were grown at 15 °C constant temperature. The mean temperature t and standard deviation St for an arbitary month is indicated to show the effect of Q_{10} on the monthly accumulated respiration.

In reactions following Arrhenius' law a straight line is obtained when the logarithm of the reaction velocity is plotted against the inverse of the temperature measured in Kelvin degrees (°C+273). The slope of the line is equal to u/R where R is the ideal gas constant and u the **activation energy**. When respiration curves are plotted this way they usually follow the Arrhenius' law, except at high temperatures where other factors may interact, like heat damage on the respiratory system or starving effects. Instead of u the ratio Q_{10} between the respiration at a given temperature and the corresponding respiration at 10 °C lower temperature, is used. In many plant species with normal growth respiration Q_{10} varies around 2.5, i.e. the respiration at 20 °C is about 2.5 times the corresponding values at 10 °C (Kramer & Kozlowski 1960, Skre 1975). The corresponding activation energy is approximately 15 000 cal/mol (Skre 1975). In growing spruce shoots an activation energy of 16 700 cal/mol was found, corresponding to $Q_{10} = 2.65$ (Skre 1972). Because of the linear relationship between respiration and growth found by Dahl & Mork (1959) one should also expect an exponential relationship between temperature and growth at low temperatures. From the correlation diagram, however, it was found that a certain basic respiration was needed for maintenance (cf. Penning de Vries 1972), corresponding to a constant temperature of 2.6 °C, and that no growth occurred below this threshold value (Skre 1972).

Additional support for dark respiration as the main limiting factor for growth was presented by Penning de Vries et al. (1974) who found good correlation between the growth of maize embryos on glucose in darkness, and the respiration loss, measured in glucose units above a certain **maintenance respiration**. The most energy-consuming maintenance processes were found to be resynthesis of proteins ("tool maintenance"), active uptake, phloem loading and osmo-regulation in leaves (Penning de Vries 1972). The conclusion was supported by McCree (1970) and Thornley & Hesketh (1972) who found that the growth respiration was proportional with the rate of substrate consumption ds/dt (growth + respiration loss) and the maintenance respiration with plant biomass W:

$$(3)\quad Rd = (1-Y_G)\, ds/dt + mY_GW$$

where Y_G is the growth yield and m the maintenance coefficient.

The existence of an alternative, cyanide-resistant respiration in tundra plants (Lambers 1980) and of increasing sink strength with decreasing temperatures in a number of plants is further evidence for **dark respiration as a growth-limiting process at low temperatures.** On an annual basis, however, photosynthesis may be limiting growth for a short period in spring, when the plants are exhausted from respiration loss during the winter (Aalvik 1939, Rutter 1957).

In Figure 4 the daily growth in leaf biomass (mg/plant) during the linear growth phase in mountain birch seedlings is shown as a function of temperature. The plants were grown at 24 hours day-length. It may be noted that at low temperatures there was an approximately exponential increase up to about 15-20 °C, in accordance with the respiration curve (see Figure 3) while at higher temperatures growth followed a typical optimum function of temperature, similar to the photosynthesis rates. The figure indicates that dark respiration may be limiting growth at low temperatures and the photosynthesis rates at high temperatures.

Respiration and tree lines. Methods are available for calculating long-term respiration equivalents based

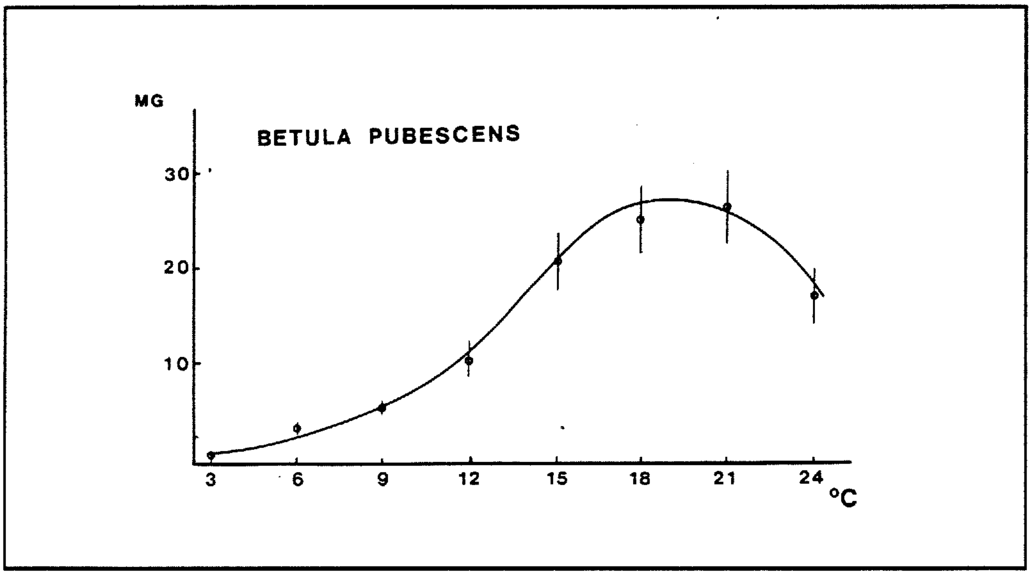


Figure 4 Growth in leaf biomass per plant (mg/day) during the linear growth phase of mountain birch seedlings from Ås, South Norway (95 m altitude) as a function of temperature at 24 hours photoperiod and 10 000 lux (300 μ Em^{-2}s^{-1}) light intensity.

on data published in meteorological summaries (Skre 1971, 1972). There is generally a linear decrease in temperatures with increasing altitudes (Werner-Johannessen 1960) varying from 0.4 °C per 100 m in winter to 0.7 °C in summer. As respiration is an exponential function of temperature, according to (3), there must be an approximately exponential decrease in the annual accumulated respiration equivalent with increasing altitude, according to (4):

$$(4) \quad \ln Re/Re_0 = kh$$

where Re_0 is the respiration equivalent above the maintenance respiration at sea level and Re the corresponding value at h metres altitude. The k-value may be found empirically by comparing meteorological stations at different altitudes, or by using a linear temperature decrease of e.g. 0.6 °C or 0.7 °C per 100 m altitude as a base for calculation. In this way maps of Re0 may be constructed to compare with isolines of timberline altitude, so-called isohypses (see Skre 1972).

Hultén (1971) has published distribution maps for all native and naturalized vascular plant species in Northern Europe. Aas (1965) and Lindquist (1949) have published distribution maps for the three main tree-line species in Scandinavia. If the supply of ATP by respiration is a limiting process, a better correlation may be expected than between distribution limits and isolines of other climatic parameters, like triterms or temperatures of the warmest month (July). It is therefore tempting to compare the horizontal distribution limits of the high temperature demanding element in the flora with isolines for respiration equivalents in spruce (Figure 9).

Coastal areas have a lower annual temperature amplitude and a longer growth period than inland areas. Plants adapted to a coastal climate would therefore be expected to have a lower Q_{10} and threshold temperature for growth than plants adapted to a continental climate. Measurements of dark respiration rates in leaf discs of elm (*Ulmus glabra*) showed a significantly lower temperature coefficient ($Q_{10} = 2.0$) than for spruce respiration and corresponding respiration rates in birch leaves of southern origin (Skre, unpubl.). Based on these experiments the respiration function of elm leaves was plotted on the diagram (Figure 3) and isolines constructed for constant annual elm respiration values at low-lying localities throughout Fennoscandia (Figure 9).

Figure 5b shows the annual spruce respiration relative to the respiration at 10 °C as a function of altitude in six different mountain areas in Scandinavia, shown in Figure 5a. Because of different k-values the slopes are slightly different. On a separate figure the corresponding diagram for elm in area A1 is shown (Figure 5c). The tree lines of spruce and mountain birch are indicated together with the limits between the low and central alpine regions and between the central and high alpine regions. The calculations are based on temperature data from low-lying and sheltered localities within the six mountain areas.

Distribution limits and the greenhouse effect. Many plants are more or less restricted by their frost sensitivity as well as their high temperature requirement, as shown by Iversen (1944) on *Hedera helix* and *Ilex aquifolium* and Fægri (1960) on a number of oceanic plants. To simplify the problem Iversen (1944) introduced a new method where plant distributions were shown on a diagram where the mean July temperatures (t_7) were plotted against the mean January temperatures (t_1) of localities where the species were present or absent. The author claimed that frost itself as well as a too short growth season may induce frost damage on the trees. The method of Iversen (1944) has proved particularly useful in studies of temperature responses in Scandinavian plants.

When the meteorological stations were plotted on such diagrams and the direction of the axis was reversed, the alpine and arctic distribution limits of a number of species appeared as straight lines with falling slopes. The reason for the falling slope is that plants need a higher summer temperature to complete their growth in a continental climate with cold winters and a short growing season than in an oceanic climate with mild winters and a long growing season. It may be shown (Skre 1979) that actual distribution limits of spruce and elm plotted on such **thermosphere diagrams** coincide with isolines respresenting certain constant annual respiration equivalents above the maintenance respiration in the two mentioned species (Figure 6). Because of its lower temperature coefficient for respiration, elm seems to be a species that is more adapted to a coastal climate than spruce and the good correlation between respiration values and actual distribution limits supports the main hypothesis about dark respiration as a limiting factor.

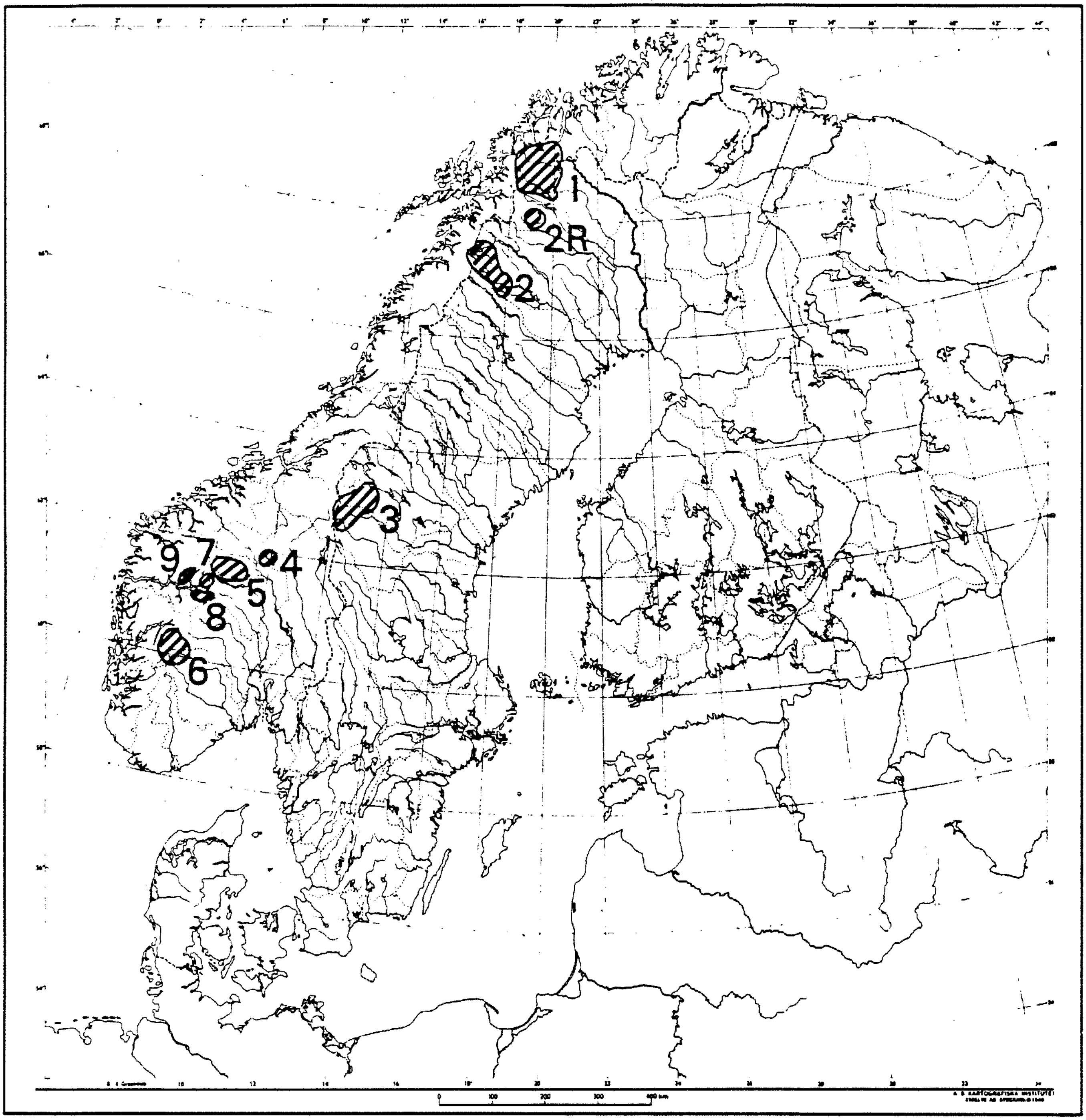


Figure 5a Mountain areas in Scandinavia where observations on altitudinal limits are available for a large number of species.

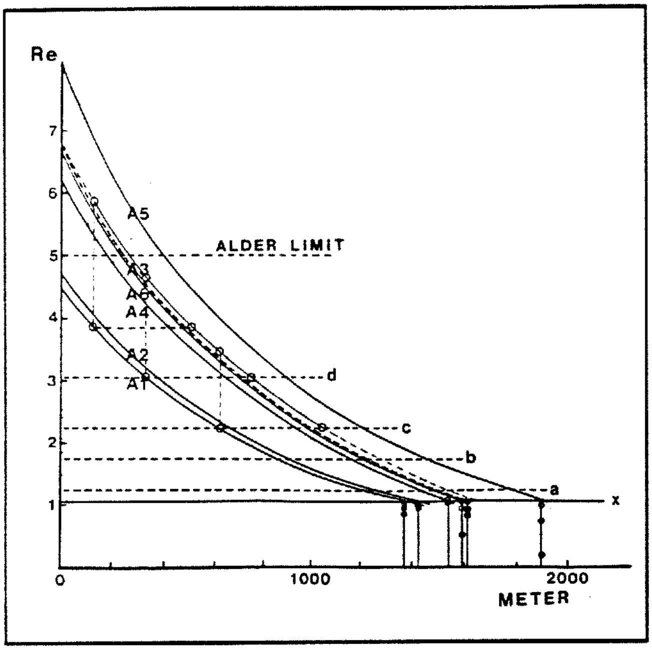


Figure 5b Annual growth respiration in spruce as a function of altitude for each of the six mountain areas shown in Figure 6a. The solid line indicates the mean common height limit in Re units for 61 alpine species where observations are available from all six areas. The dashed lines show the limits between the high and central alpine region (a), the central and low alpine region (b), the birch limit (c) and the spruce limit (d).

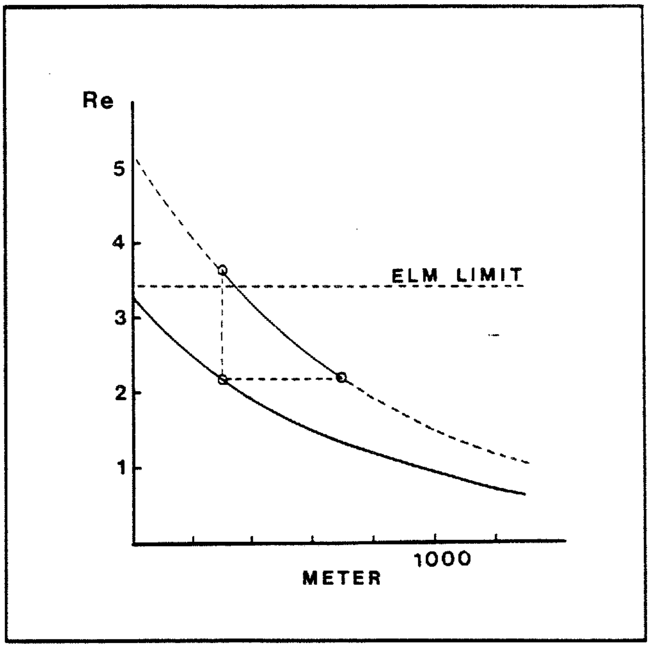


Figure 5c Annual growth respiration in elm at sheltered localities as a function of altitude in inner Troms, North Norway (A1). The tree line of elm is indicated (dashed line).

In Figure 6a-b the isolines corresponding to discrete values of annual respiration units in spruce shoots and elm leaves are also plotted. From the exponential relationship between respiration and temperature one would expect that the rise in corresponding annual respiration equivalents would decrease with increasing July temperature. This is not the case, in fact there seems to be an almost linear relationship between t_7 and Re (see Figure 6c). The reason is probably that the vertical temperature decrease is much lower in the summer season than in winter, due to increased solar radiation and instability in the air. According to Werner-Johannessen (1960) this vertical decrease varies from 0.4 °C per 100 metres in summer to 0.7 °C in winter. The July temperature, like the annual respiration, is also more influenced by local topography, the so-called "Massenerhebung", than other temperature measurements (Skre 1972).

If now the winter temperatures are raised by 4 °C and summer temperatures by 2 °C as stated in the scenario, the distribution limits will move towards more arctic and alpine areas, partly because of higher respiration rates in summer and partly because of a longer growing season, represented by a higher January temperature. The effect of a higher winter temperature will tend to be stronger in a plant with an oceanic distribution and a low temperature coefficient for growth like elm (*Ulmus glabra*) than in plants like Norway spruce (*Picea abies*) or mountain birch (*Betula pubescens*) with a high temperature coefficient. This may be seen from Figure 7 where the expected temperature rise is for plotted two localities close to the tree lines of the last two species. From Figure 6 the increase in spruce respiration was found to be 1.47 units, corresponding to 2.6 °C higher July temperature, and in elm 1.55 units, corresponding to 3.0 °C higher temperature. From Figure 4 it may be seen that as a result of the expected climatic change **the spruce distribution limit will be raised by about 400 m, and the birch limit by 450 m.** Because of the exponential increase in annual respiration values with temperature, the difference in altitude corresponding to one annual respiration unit increases

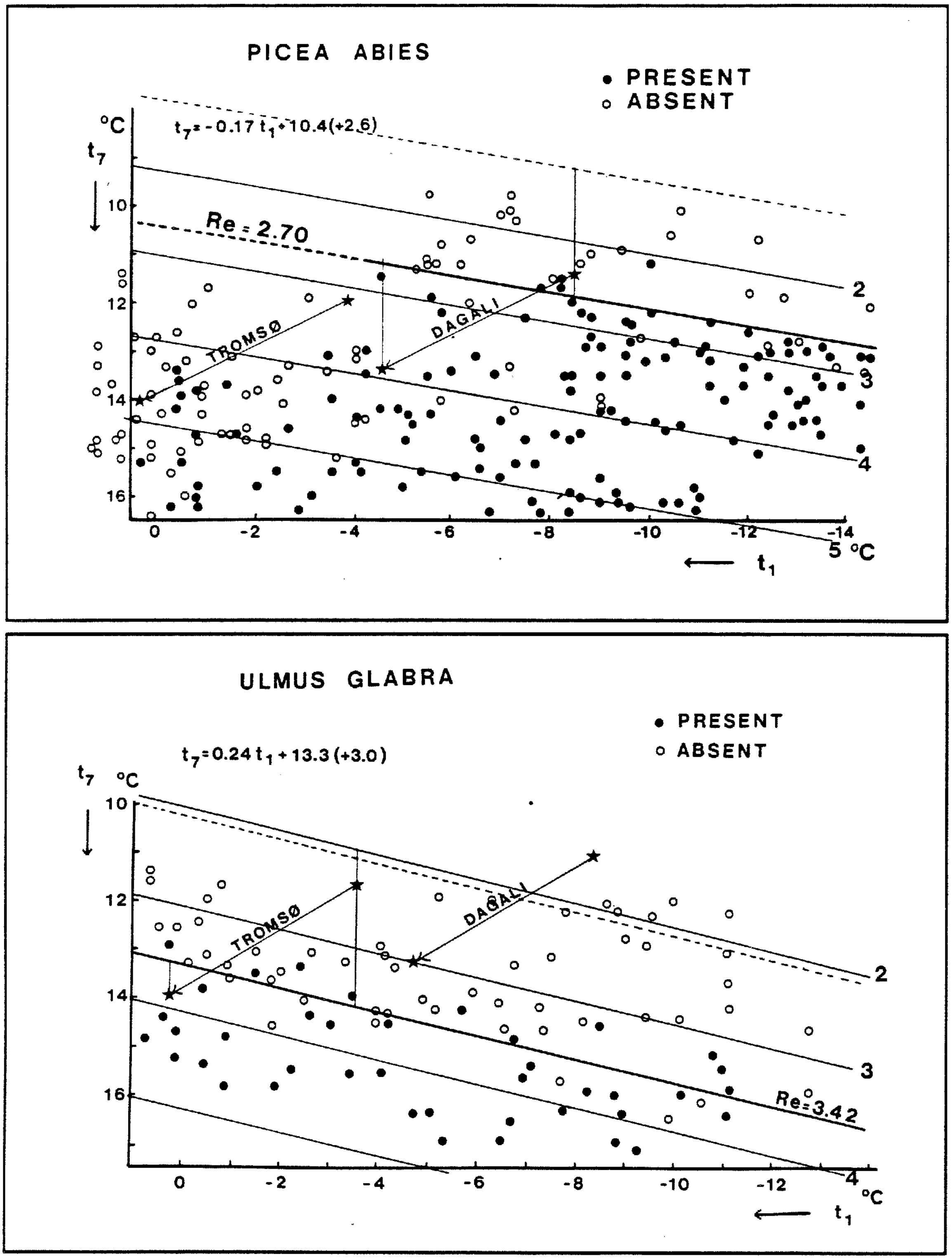
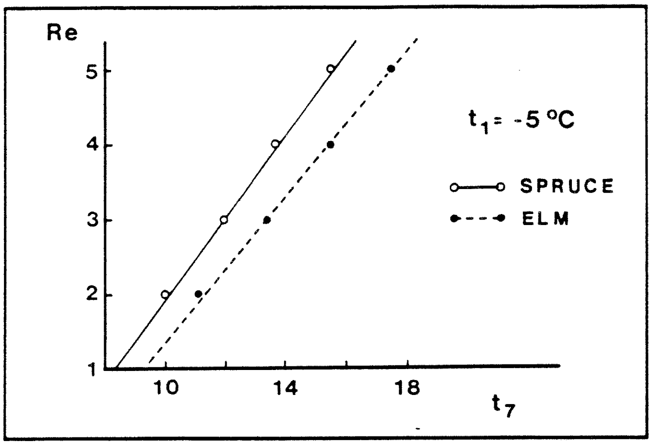


Figure 6 The distribution of *Picea abies* (a) and *Ulmus glabra* (b) shown in a thermosphere diagram where the mean January temperatures (t_1) are plotted against the corresponding July temperatures (t_7). The distribution limits (except for natural regenerated spruce in West Norway) coincide with isolines representing a constant accumulated annual growth respiration equivalent to 2.70 and 3.42 units respectively, based on the values in Figure 3. Main isolines and the effects of an expected temperature rise of +2 °C in t_7 and +4 °C in t_1 on the distribution limits are indicated. The relationship between annual respiration rates in spruce shoots and elm leaves, and the corresponding July temperatures at -5°C January temperature, are shown on a separate figure (c).



with altitude. The distribution limit of *Alnus glutinosa*, a lowland species with higher temperature demands, is expected to rise by only 300 m. In *Ulmus glabra* the low temperature coefficient will cause a relatively large rise in the tree line, about 350 m (Figure 5c).

Another result of the greenhouse effect is a longer growing season and higher winter temperatures, and correspondingly higher respiration loss during the winter. The shortening of the frost-free period is expected to be much greater at oceanic tree-line localities than at continental localities. Because winter temperatures will increase more than summer temperatures, the effect of climatic change is expected to be mostly through a shortening of the dormancy period. In Figure 7 the annual temperature distribution is shown at two localities (Bruun 1967). One locality, Dagali, is located at an altitude of 887 m in a continental area in South Norway (60° 15'N) close to the spruce timberline while the other locality, Tromsø, is located near sea level in North Norway (69°39'N). The summer temperatures at Tromsø are only slightly higher than at Dagali while winter temperatures are about 5 °C higher (see Table 1). The growth period varies from 165 to 180 days at Dagali and from 195 to 220 days at Tromsø when the threshold temperatures for growth t_b = 2.6 °C and 1.5 °C in the two species are taken into account. After the expected climatic change has taken place Dagali will have changed to almost the same climate as Tromsø has today with slightly higher summer temperatures (t_7 = 13.4, t_1 = -4.6) and Tromsø to a climate similar to Bergen today (t_7 = 14.0, t_1 = 0.4). The growth period will increase to 210-280 days at Dagali and 225-315 days at Tromsø, the highest values referring to elm. In the lower part of the figure the monthly respiration equivalents of the two species are shown, based on the diagram in Figure 3. Because of the much higher temperature coefficient of the dark respiration function, the expected 2 °C temperature increase in summer will have a much stronger effect on spruce shoots than on elm leaves, as also shown in Table 1. The table also shows that

Table 1 The mean January (t_1) and July (t_2) temperatures in centigrades (°C), length of the growth period V_1 and V_2 in days and annual growth respiration in spruce shoots (Re_1) and elm leaves (Re_2) at Dagali and Tromsø before and after the expected climatic change (cf. Figure 7). Tree-line respiration values and threshold temperatures for growth t_b (°C) are indicated in the lower part of the table.

	Dagali						Tromsø					
	t_1	t_2	V_1	V_2	Re_1	Re_2	t_1	t_2	V_1	V_2	Re_1	Re_2
Before	-8.6	11.4	165	180	2.38	1.97	-3.6	12.0	195	220	2.85	2.63
After	-4.6	13.4	210	280	3.81	3.01	0.4	14.0	225	315	4.71	4.16

	Elm leaves	Spruce shoots
Tree-line R_e	3.42	2.85
t_b (°C)	1.5	2.6

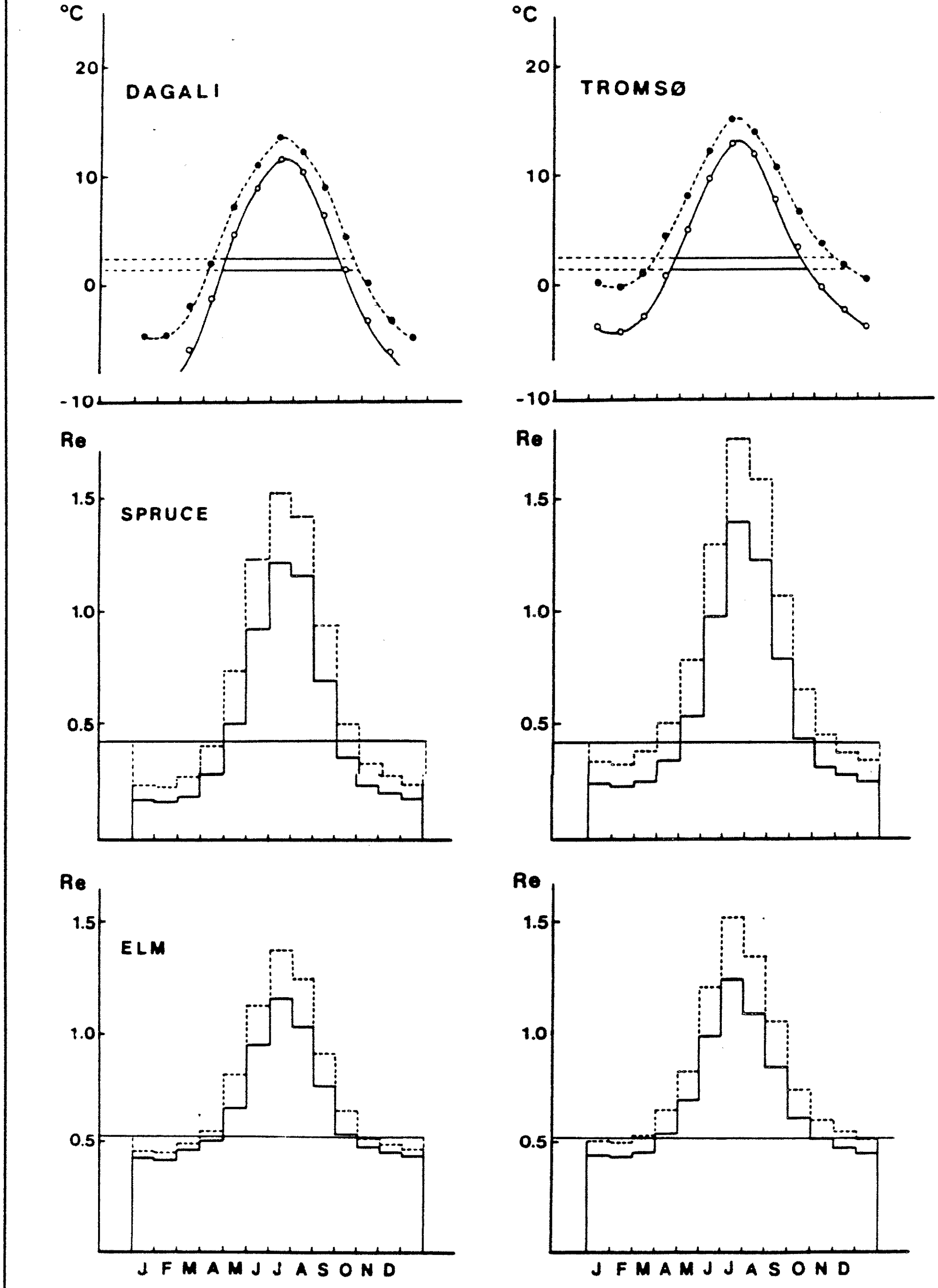


Figure 7 The annual temperature distribution at Dagali and Tromsø (top) compared with the monthly respiration equivalents in spruce (centre) and elm (bottom). The consequences of a temperature rise of +2 °C in summer and +4 °C in winter are indicated (dashed lines). Horizontal lines indicate the threshold temperatures for growth t_b (see Table 1) and the maintenance respiration Re_m in the two species.

the temperature rise willhave a stronger effect on respiration rates in both species at Tromsø than at Dagali because of higher temperatures at the former station.

As a conclusion, Table 1 and Figure 7 show that the expected climatic change will bring both stations well below spruce timberlines (see also Figure 9), and Tromsø will also be situated within the distribution limit of elm.

To investigate the influence of the expected climatic change on the respiration loss during winter and the physiological status of the trees, some results are shown from a field experiment comparing mountain birch seedlings grown in fertilized peat on an oceanic lowland site at Fana (50 m) and on a tree-line site at Kvamskogen (450 m altitude). A comparison between the sites (Figure 8) show approximately twice as high growth rates at the former locality. The difference between the lowland and tree-line sites increased as the plants were growing, because birch like many other deciduous species (cf. Prudhomme 1983) are rather **opportunistic species**, in that a relatively large part of the energy from respiration is invested into new growth of structural and photosynthetic tissue. By increasing their photosynthetic capacity, plants are able to replace some of the carbohydrates that were consumed in the growth process (see Thornley 1972), this tendency is usually strongest in the fast growing southern ecotypes. The second year (1987) growth rates at the lowland site of Fana had increased to about four times the corresponding growth rates at Kvamskogen in lowland birch and southern ecotypes of mountain birch seedlings. In the northern ecotype from Finnish Lapland (BJ), on the other hand, there was almost no altitudinal effect, the growth was much slower and the photosynthetic products were invested into storage products and root growth. There are also indications that arctic populations "burn off" part of their stored energy through alternative respiration simply to avoid growth and keep a high concentration of nutrients in their tissue (Chapin 1979, Skre 1990). Parallel to the much higher growth rates at the lowland site, however, there was also a much higher respiration loss during the winter. The amount of non-structural carbohydrates in roots dropped from 40 % to 15 % dry weight at Fana and only to 25 % at Kvamskogen, indicating lower sink strength at the former site. The expected temperature rise due to the greenhouse effect would therefore not only result in much higher growth rates but also in lower sink strength and available energy resources, particularly in fast-growing species and ecotypes. If the process goes too fast, the time will be too short for plants to develop new ecotypes that are adapted to the new climate. **The photosynthesis will take over as the growth-limiting process at ambient field temperatures** and many plants will therefore be restricted not only by their upper distribution limit but also by a lower limit. Printz (1933) suggested that high winter temperatures might restrict spruce growth in West Norway, but his theory was later rejected (Hagem 1947). However, future climatic change might again actualize a situation like the one predicted by Printz (1933).

Summary

In alpine and arctic areas where climate is constantly changing between a cold and a warm season, most plants will have evolved methods to survive the unfavourable season. During the year plants are subjected to many kinds of damage. To repair this and protect the living tissue against new damage, and for reproduction, growth and active uptake in roots, energy is needed by the production of ATP through photosynthesis and respiration. For this reason plants growing close to their distribution limits will be restricted by certain high temperature demands to complete their life cycle and to produce viable seeds and/or winter buds.

To account for the observed requirements for high temperature, various empirical parameters have been introduced. The most common one is the so-called heat sum, i.e. the accumulated temperature above a certain threshold value. The tetraterm, i.e. the mean temperature during the four warmest months of the year, has been widely used in forestry to express the high temperature demands for seed ripening in trees. However, for a satisfactory explanation of a distribution limit a good correlation, as well as a physiological mechanism explaining the correlation, is needed. One such mechanism is the dark respiration. The respiration rates in growing shoots of spruce have been found to correlate well with the daily apical growth at low and medium temperatures above a certain threshold value, and similar relationships have been found in leaf discs of birch and elm, and in maize embryos. The existence of an alternative, cyanide-resistant respiration in tundra plants and of increasing sink strength with decreasing temperatures in a number of plants is further evidence for dark respiration as a growth-limiting process at low temperatures. On an annual basis,

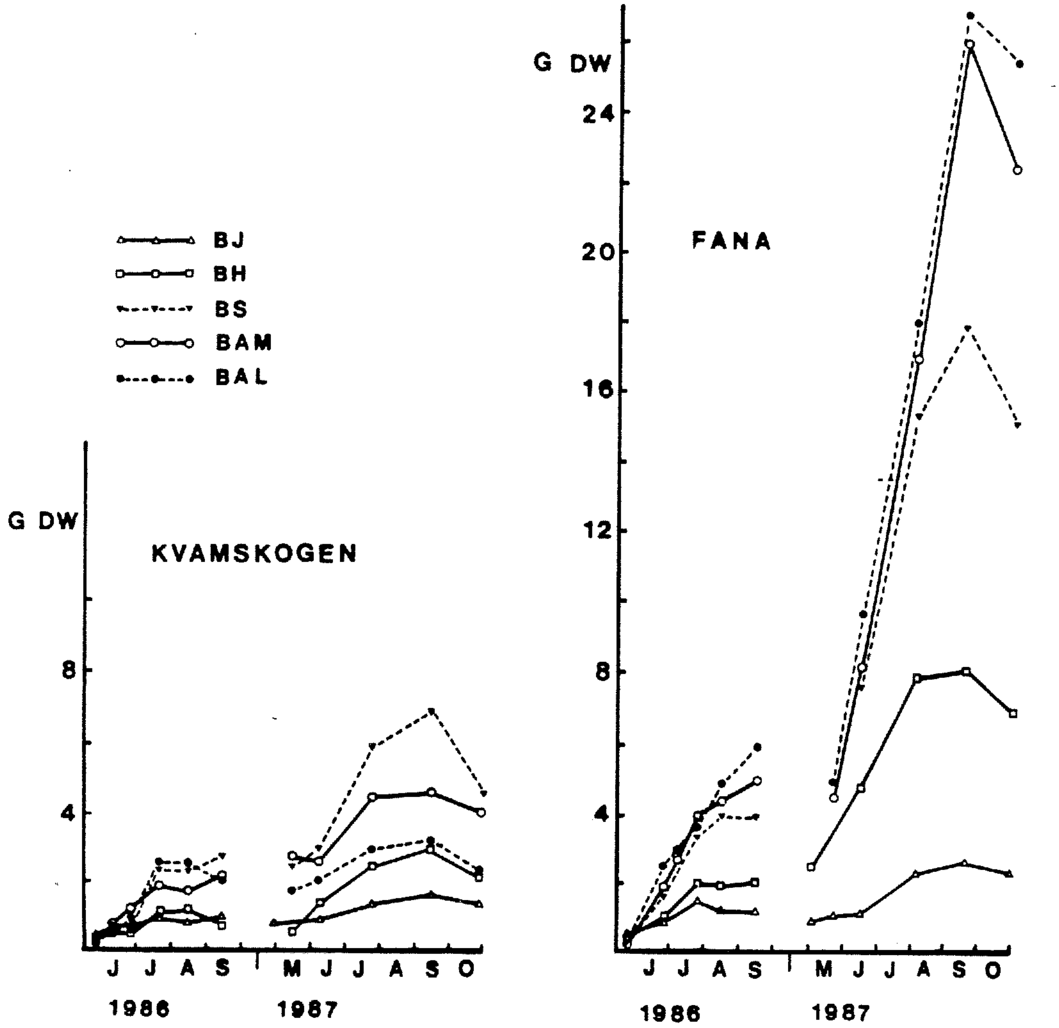


Figure 8a Biomass (mg/plant) of mountain and lowland birch seedlings grown in fertilized peat from the 4-leaf stage during the 1986 and 1987 seasons at Fana (50 m) and Kvamskogen (450 m altitude). The ecotypes are:

Betula pubescens: BJ Kevo, North Finland (200 m), BH Blefjell, Central Norway (750 m), BS Fana, West Norway (50 m), BAM Løten, East Norway (200 m). *B. pendula*: BAL Løten, East Norway (200 m).

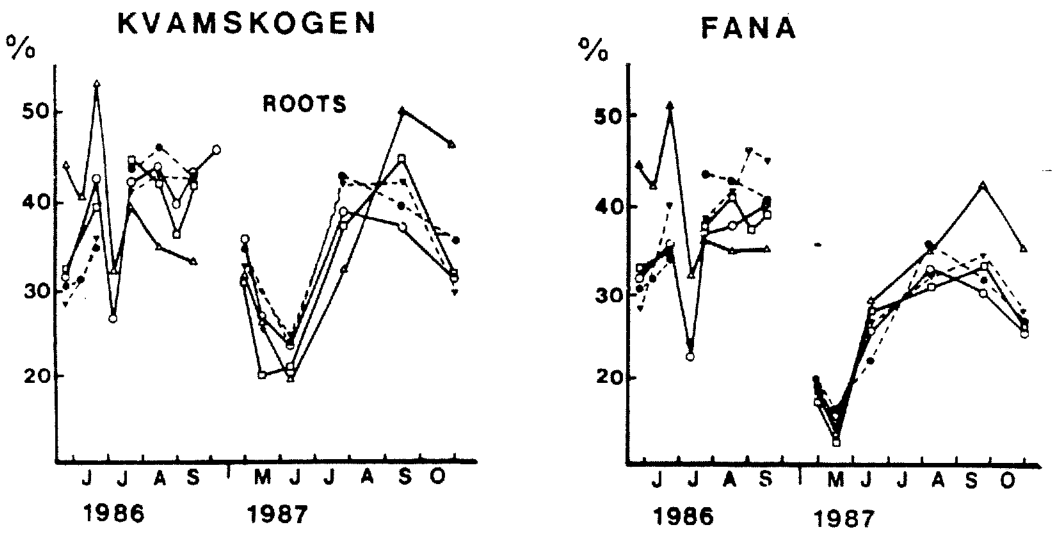


Figure 8b Total non-structural carbohydrate content (% dry weight) in roots of birch seedlings at Fana and Kvamskogen during the 1986/87 seasons. See Figure 8a for explanation.

however, photosynthesis may be limiting growth fora short period in spring when the plants are exhausted from respiration loss during the winter.

Methods are available for calculating long-term respiration equivalents based on data published in meteorological summaries. There is generally a linear decrease in temperature with increasing altitude. As respiration is an exponential function of temperature, this means that the annual accumulated respiration equivalents show a general exponential decrease with altitude. In this way maps of annual respiration at sea level or at low-lying localities within restricted areas throughout Fennoscandia may be constructed.

When the mean July temperatures are plotted against the mean January temperatures, the alpine and arctic distribution limits of a number of species appear as straight lines with falling slope when the directions of the axis are reversed. It can be shown that in spruce shoots and leaf discs of elm these lines coincide with isolines representing certain constant annual respiration equivalents above the maintenance respiration. The reason for the falling slope is that plants need a higher summer temperature to complete their growth in a continental climate with cold winters and a short growing season than in an oceanic climate with mild winters and a long growing season. If the winter temperatures are raised by 4 °C and summer temperatures by 2 °C, as stated in the scenario, the distribution limits will move towards more arctic and alpine areas, partly because of higher respiration rates in summer and partly because of a longer growing season, represented by a higher January temperature. The effect of a higher winter temperature will tend to be stronger in a plant with an oceanic distribution and a low temperature coefficient for growth like elm (*Ulmus glabra*) than in plants like Norway spruce (*Picea abies*) or mountain birch (*Betula pubescens*) with a high temperature coefficient. The expected increase in spruce respiration is 1.56 units, corresponding to 2.65 °C higher July temperature, and in elm 1.75 units, corresponding to 2.97 °C higher temperature. At tree-line altitudes this corresponds to about 500 m vertical difference.

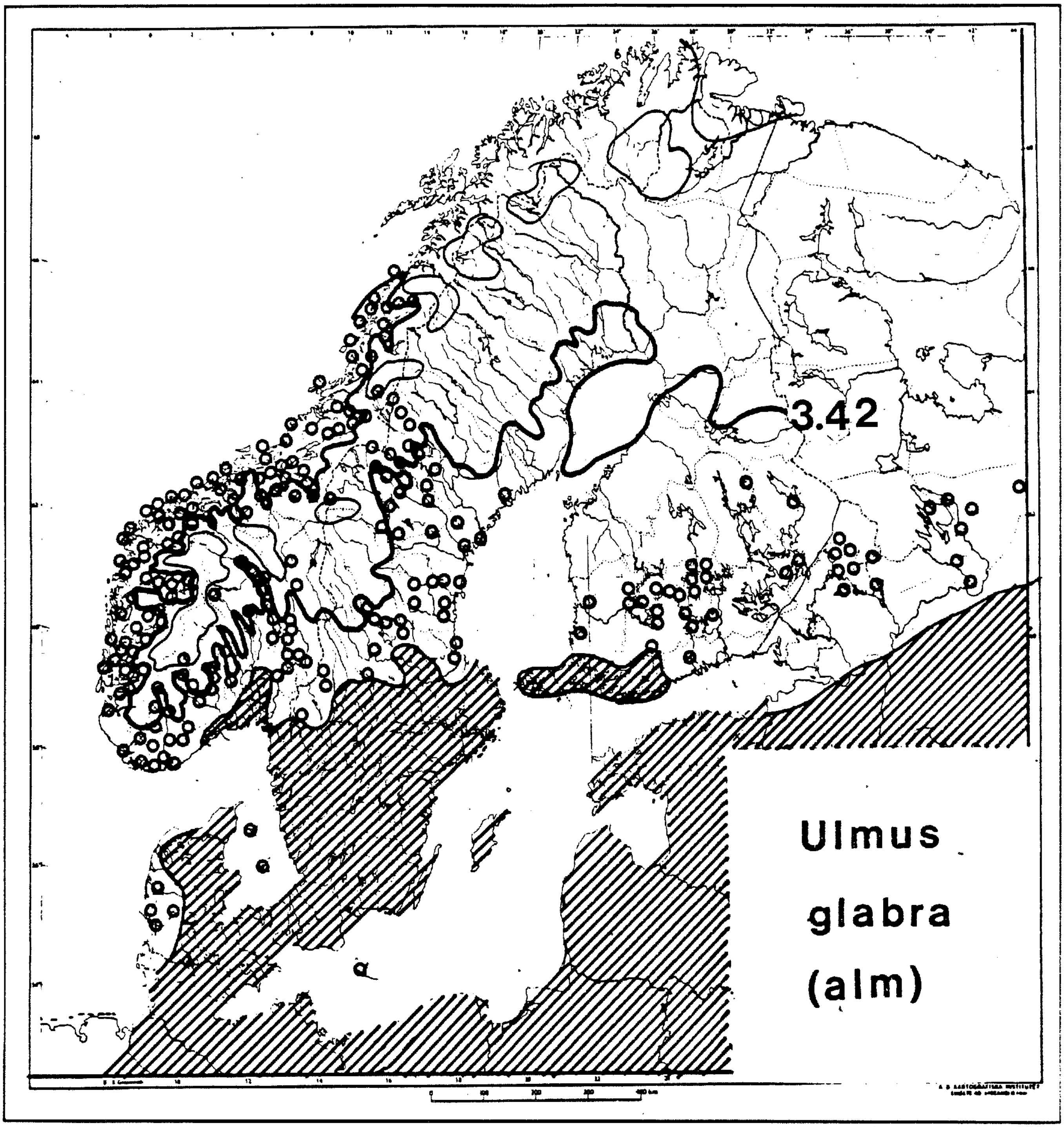
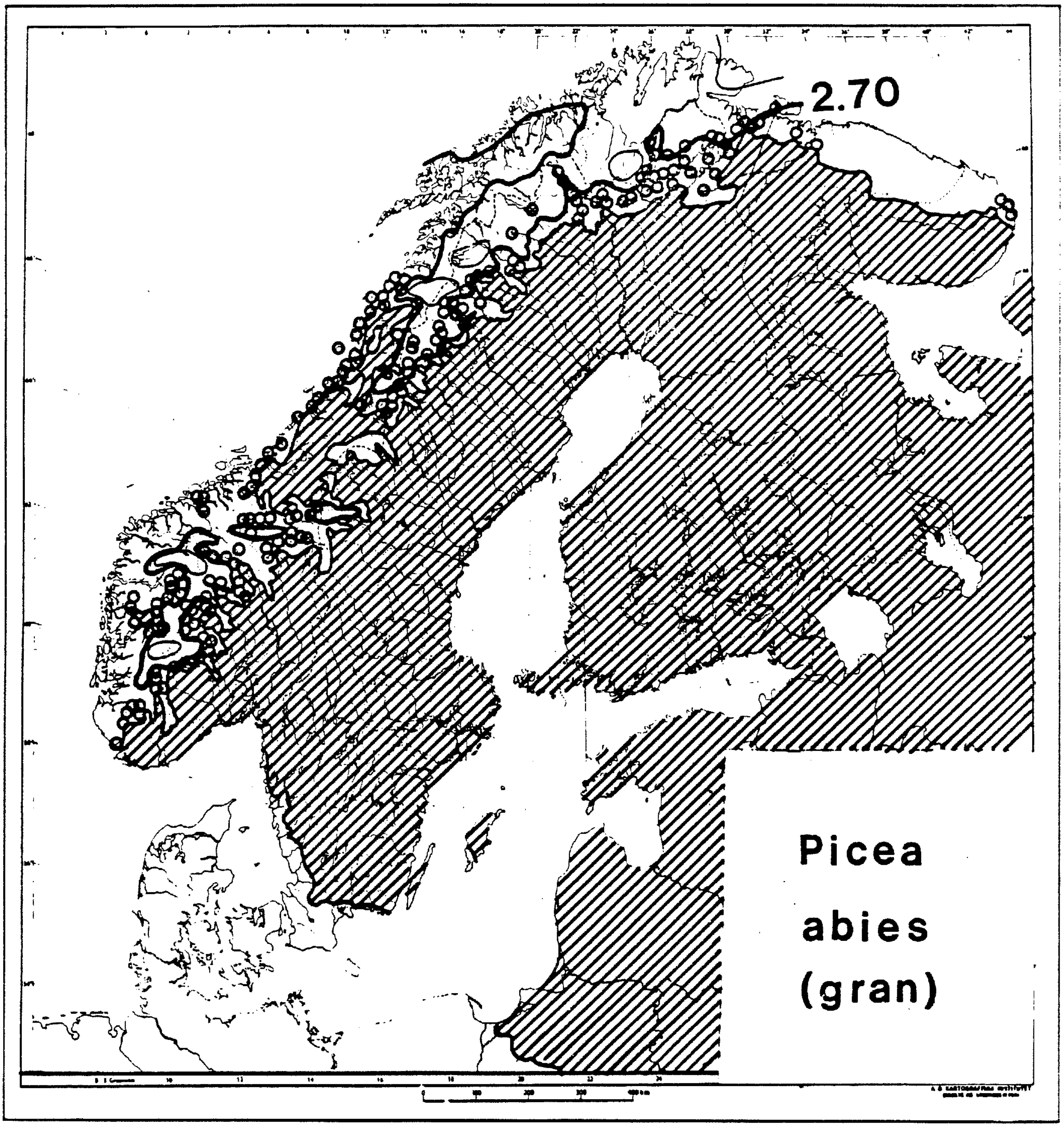
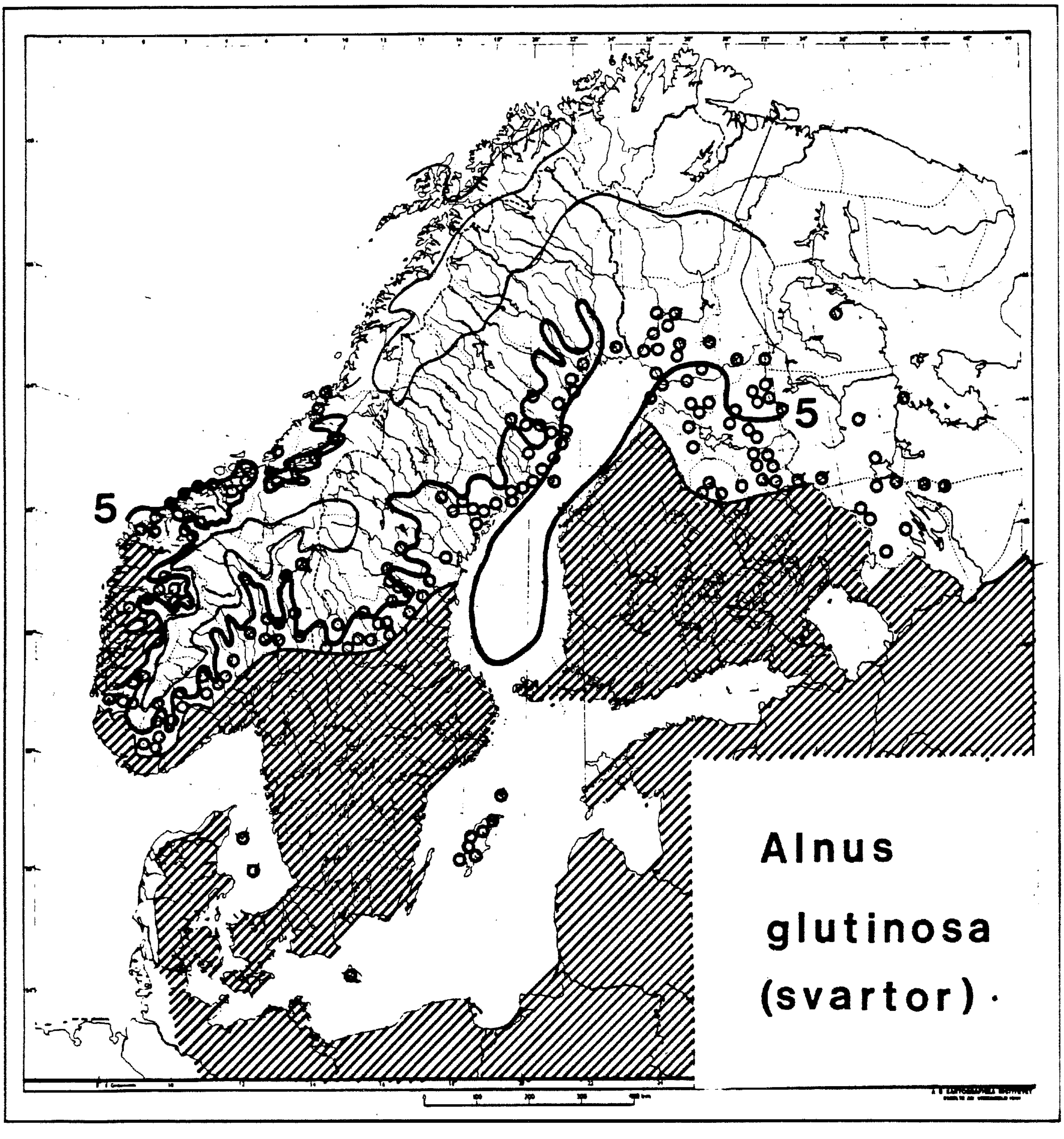


Figure 9 Distribution maps of *Ulmus glabra* (a), *Picea abies* (b) and *Alnus glutinosa* (c) showing the present distribution and the annual respiration equivalent (relative units) corresponding to the present alpine distribution limit (solid line) and the distribution limit after the expected climatic change (dashed lines).


2.70
Picea
abies
(gran)



Alnus glutinosa (svartor).

Another result of the greenhouse effect, however, is a longer growing season and higher winter temperatures, and correspondingly higher respiration loss during the winter. The shortening of the frost-free period is expected to be much higher at oceanic tree-line localities than at continental localities. A comparison between mountain birch seedlings grown in fertilized peat on an oceanic lowland site at Fana (50 m) and on a tree-line site at Kvamskogen (450 m altitude) showed approximately twice as high growth rates at the former localtity. The difference between the lowland and tree-line sites increased as the plants were growing, especially for the fast-growing southern ecotypes. On the lowland site, however, there was also a much higher respiration loss during the winter. The amount of non-structural carbohydrates dropped from 40 % to 15 % dry weight at Fana and only to 25 % at Kvamskogen, indicating lower sink strength at the former site. The expected temperature rise due to the greenhouse effect will therefore not only result in much higher growth rates but also in lower sink strength and available energy resources, particularly in fast-growing species and ecotypes. If the process goes too fast, the time will be too short for plants to develop new ecotypes that are adapted to the new climate. The photosynthesis will take over as the growth limiting process at ambient field temperatures and many plants will therefore be restricted not only by their upper distribution limit but also by a lower limit.

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Adaptation and adaptability in Scandinavian plants

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The genetic variability within species is great, both in morphological and physiological characters (Table 1a, 1 and Figures 2, 3, 4, 5).

Prior to the 1950s, much of the research work in this field was concerned with showing that morphological genotypes were characteristic of different habitats. Recently, more research has been directed towards physiological differences within species and the development of physiological ecotypes. This type of research is very important at a time with changing climatic conditions and increased air and soil pollution especially in our cities, industrial areas and so forth.

In addition, modern propagation and production techniques combined with efficient marketing have spread homogeneous plant materials over a range of climatic regions in Europe (Figure 1). Such plant materials may be poorly adapted to environmental conditions different from those at the origin of the genotypes. This lack of adaptation again leads to reduced survival and increased maintenance cost for the plantings. This is a problem of particular importance for the north Scandinavian countries where the environmental conditions are so different from those in the main part of Europe and because of the extensive import of landscape and ornamental plants from those climatic regions. For instance, in Norway more than 90 % of the plant material is of southern origin thus creating great winter survival problems (Table 1).

Table 1. Winter survival (%) of ecotypes of Betula pubescens Ehrh. cultivated at lat. 60°N, 64°N and 70°N.

	% Survival Lat. of cultivation		
Lat. of ecotype	60°N	64°N	70°N
56°N	85	45	0
63°N	95	100	35
70°N	55	90	100

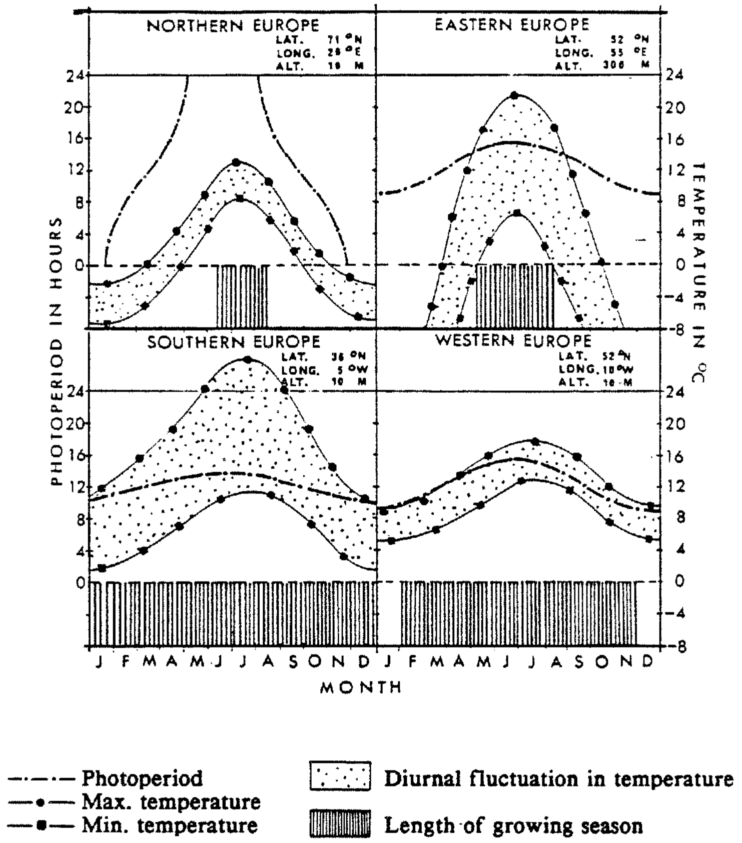
Table 1a. Family variation in germination, establishment and % saleable plants in some important ornamental species.

	Germination %		Establishm. %		% saleable pl.	
Species	Max	Min	Max	Min	Max	Min
Acer platanoides	80	5	100	30		
Amelanchier spicata	82	22	92	48		
Betula pendula	58	0	90	11	95	15
Prunus avium	94	18	95	47	91	35

Both the changing environmental conditions and the increased international trade with plants make the adaptability or stability of different genotypes, families or populations to a very important factor both in natural ecosystems and commercial varieties. Certain habitats, owing to a mixed and rather low level of selection pressure, are able to preserve a great range of variability within a population and to produce genotypes which can tolerate variable climatic conditions, while others will exclude all but the specialized, highly adapted variants of the population (Harland & Martin 1938, Håbjørg 1976). The stability of a certain population or genotype or rather its ability to develop satisfactorily under differing climatic conditions is a decisive qualification for native plant populations in a situation with changing environmental conditions, but also for genotypes/varieties in countries so sparsely populated and with such great climatic variations as in Norway. Here the growing season can vary from less than 3 months in the northeast, with practically continuous light during the growing season, to more than 9 months in the southwestern part of the country and with daylengths varying from 12 to 18 hours. In addition, the maritime climate in the west and the continental climate in the east causes great fluctuations in temperature. In the most continental areas in the northeast, the **maximum difference** between summer and winter temperature is more than 80 °C (+30 to -50 °C) and in the maritime areas in the southwest less than 35 °C (+25 to -10 °C).

Adaptation to important climatic and edaphic factors. During the last 15 years a number of experiments have been carried out under controlled climatic conditions in a phytotron at the Agricultural University of Norway and in regional field experiments at 5-8 different locations in Norway to study

Figure 1 Some climatic data and length of the growing season at the most extreme northern, southern, western and eastern towns in Europe.



the responses of maritime, continental, southern and arctic ecotypes to important climatic and edaphic factors. So far adaptation to the following environmental factors has been found.

1 Climatic factors
  Light intensity
  Light quality
  Photoperiod
  Temperature (Optimal/Min/Max) for growth
  Differences in temp. requirement during the dormancy period
  Air humidity
  Air pollution
2 Edaphic factors
  Soil pollution
  pH (calcium content)
  Nutritional stage
  Heavy metal tolerance

In the following only the most important factors will be discussed.

Photoperiod is obviously the most important factor controlling growth and development of most plant species in the north temperate and arctic regions, and it is especially so for the onset of growth cessation. In an extensive ecotype study on 13 woody ornamentals and two grass species, all spontaneous to Scandinavia and collected at three different latitudes, 56°N, 63°N and 70°N and at different altitudes, it was shown that all species except one responded strongly to photoperiod.

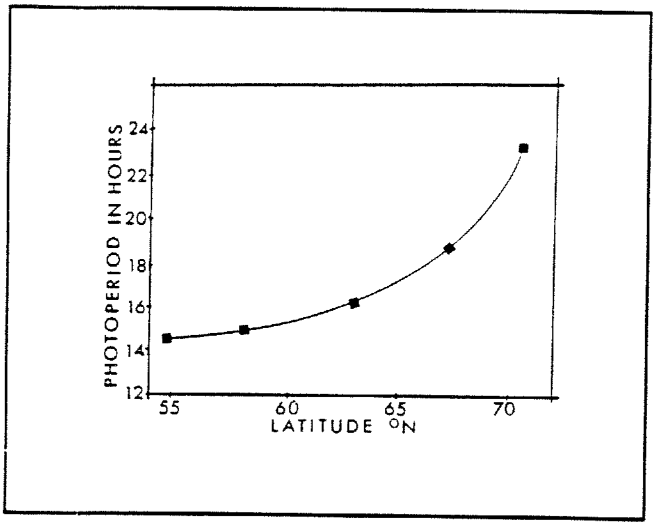
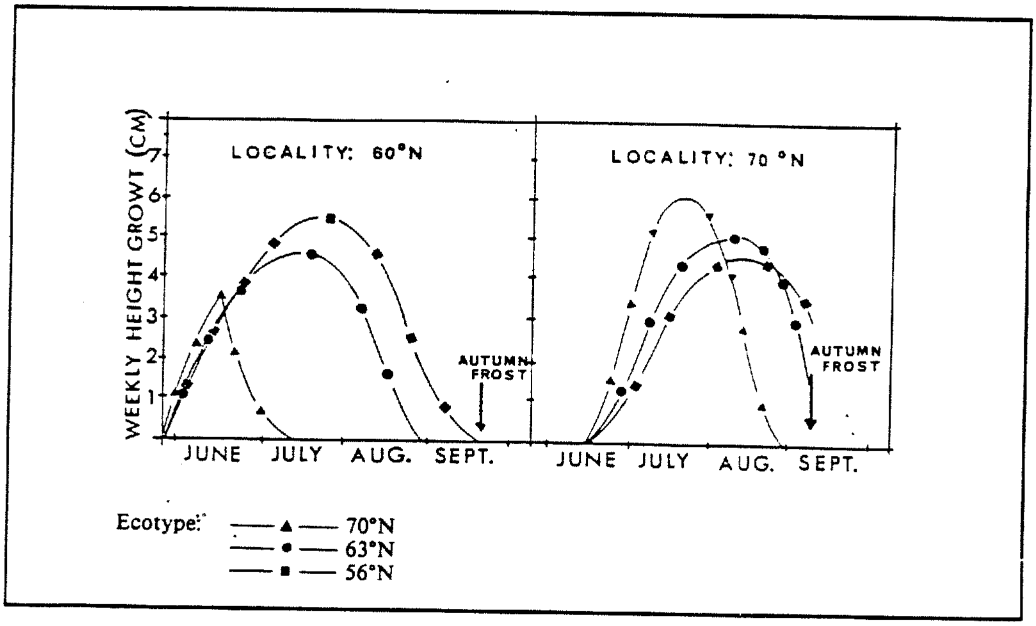


Figure 2 Critical photoperiod for vegetative growth in latitudinal distant ecotypes of thirteen woody species.

The critical photoperiod for shoot elongation varied considerably among ecotypes (Håbjørg 1972a, 1976, 1978). It was, however, almost the same for identical ecotypes of different woody species and 1 to 2 hours shorter for grass ecotypes (Figure 2). The very strong photoperiodic control of growth in Scandinavian plant materials makes it difficult to grow northern ecotypes in southern areas. As demonstrated in Figure 3, north Scandinavian ecotypes of *Betula pubescens* completed growth already in July with a shoot growth of 10-12 cm when grown at 60°N. Grown at their origin 70°N, they had a seasonal shoot elongation of 45-50 cm or slightly more than southern ecotypes. Further experiments have shown that the photoperiodic control of growth and development gradually became less important in southern and more maritime ecotypes, and it was also evident that growth cessation in species with an early growth cessation like *Fraxinus*, *Syringa* and *Sorbus* seemed to be little affected by photoperiod. In fact, field experiments carried out at 59, 63 and 71°N showed that northern ecotypes of *Sorbus aucuparia* had about the same yearly shoot elongation at all localities, 30-35 cm.

Light intensity/quality vary seasonally, diurnally and with the habitat, latitude, altitude, and aspect. It is evident that great differences exist between ecotypes in photosynthetic light acclimatisation. Ecotypes native to open habitat and to densely shaded areas showed that "shade types" did not acclimate to high light conditions (Bjørkman & Holmgren 1963).



Fiigure 3 Weekly height growth of three latitudinally distant ecotypes of *Betula pubescens* Ehrh. cultivated at two localities - 60°N.

Differences in response to light intensity and light quality are also found for photoperiodic reactions. In studies under controlled environmental conditions (Håbjørg 1972b), north Scandinavian ecotypes had a critical light intensity for photoperiodic responses of 250 to 500 lux and south Scandinavian ones 15-100 lux (Figure 4). Northern ecotypes also required a greater percentage of red light, thus indicating a difference in "measuring" the day-length. Ecotypes from northern parts of Scandinavia seem to measure the day-length from sunrise to sunset while southern ones also include part of the twilight.

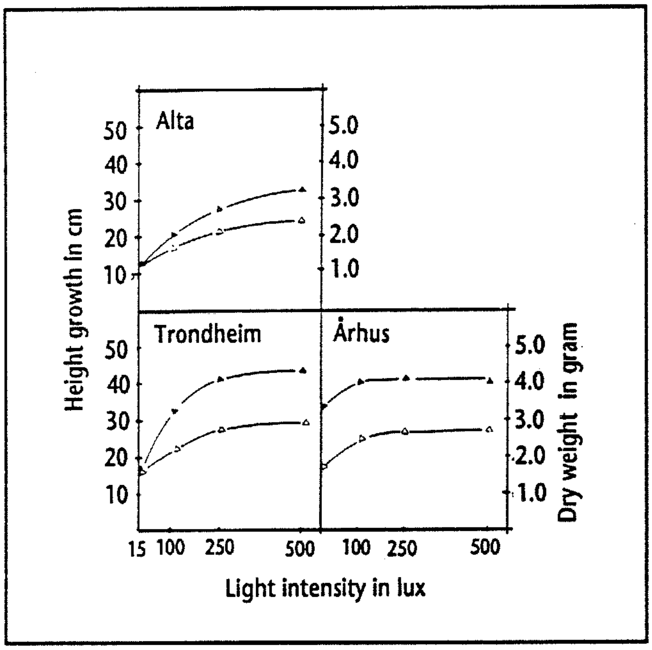


Figure 4 Effect of light intensity on shoot growth and dry weight of latitudinal ecotypes of *Betula pubescens.*

Temperature is an important factor for plant growth, and it strongly affects/modifies all light reactions within the plant (Håbjørg 1972a). As shown in Figure 1, the vegetation in Europe is subjected to wide seasonal and diurnal temperature fluctuations. Marked differences are found among species and ecotypes in their response to optimum and minimum temperatures for growth and development. Ecotype studies on North European trees have demonstrated adaptation to diurnal temperature fluctuations. Ecotypes from maritime and northern areas, where the diurnal temperature fluctuations are smaller than in southern and continental areas (Figure 1), also reached their optimum shoot growth when exposed to smaller fluctuations in diurnal temperatures (Figure 5).

Under Scandinavian conditions, differences among ecotypes in response to low temperature stress is crucial. As demonstrated in Figure 3 and Table 1, the response to low temperature stress in the autumn is always strongly related to the physiological conditions of the plant at the moment of the first autumn frost. However, early autumn frost damage is not the only crucial moment for winter survival for plants in Scandinavia. Stability in winter-frost resistance is, as demonstrated in Table 2, extremely important.

Arctic and continental ecotypes adapted to highly specialised and stable winter conditions showed a very strong reduction in winter survival when grown under maritime and southern conditions or at localities with unstable winter conditions. On the other hand, the fjord types exposed to a mixed selection

Figure 5 Effect of night temperature on shoot growth and dry weight of latitudinal ecotypes of *Betula pubescens.*

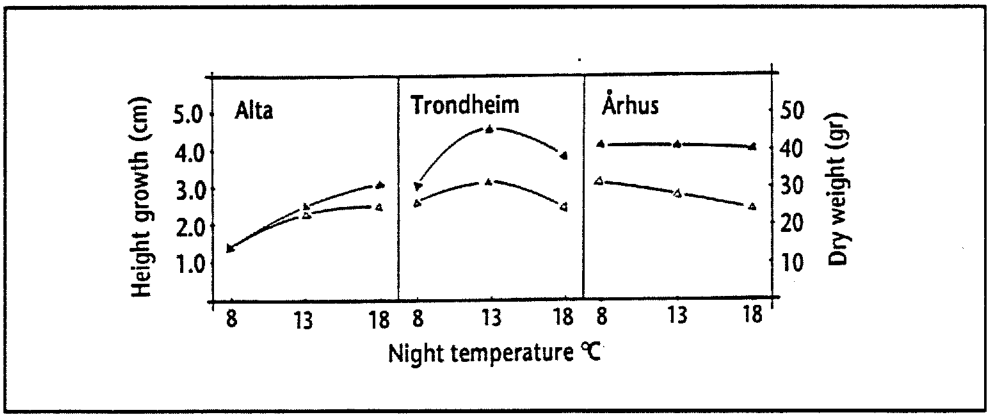


Table 2. Differences in adaptability/stability between ecotypes of *Poa pratensis* (% survival).

	Place of cultivation			
Ecotype	Arctic 70°N	Southern 58°N	Maritime	Continental
Arctic 70°N	90	10	0	70
Southern 53°N	10	90	90	50
Fjord-type	70	70	90	80
Continental	85	25	40	90

pressure at their place of origin with both maritime and continental climate, also produced very stable ecotypes which could survive and grow fairly well under both maritime and continental conditions. The difference in stability in winter-frost resistance seemed, according to experiments under controlled climatic conditions, to be related to differences in chilling requirement (Table 3). The maritime ecotypes of *Picea abies* from coastal areas in Trøndelag needed about 2 weeks longer chilling treatment at 2 °C to break bud dormancy than the more continental ecotypes from the same latitude.

Table 3. Ecotype differences in bud-breaking conditions of Picea abies (% bud break)

	Weeks at 2°C					
Ecotype	0	1	3	5	7	9
Maritime	0	0	2	26	91	99
Continental	0	0	18	98	97	99

The **stability in winter-frost resistance** obviously is of increasing importance in Scandinavia because of the warmer winter climate. The last 2-3 years of changing winter climate in the southern part of Norway has caused severe damage to typical continental species like *Ribes alpinum* and *Berberis thunbergii*. In northern Norway, in the town centres of Tromsø and Narvik, a frightening tree damage/-death of local ecotypes of *Betula pubescens* and *Sorbus aucuparia* has been registered. The damage must partly be due to the unusually warm and unstable winter climate and the lack of stability in winter-frost resistance of the local ecotypes. Extensive cambium damage indicated that the ecotypes had gone through the dormancy period and started growth in late autumn, and were subsequently damaged by a succeeding frost period. More maritime tree species like, for instance, *Acer pseudoplatanus*, which ordinarily are not considered so hardy, showed no damage. Heavy traffic pollution affecting the depth of the dormancy may also account for part of the damage.

Air and soil pollution damage to vegetation is probably the most important abiotic stress factor in urban and trafficked areas. For instance, measurements of lead accumulation on leaves of different species along highways in Norway showed that plant species with hairy and/or strongly wrinkled leaves like *Corylus avellana* and *Ulmus glabra* accumulated 3-4 times more pollutants than species with smooth leaves like *Syringa vulgaris*. Observations made on vegetation in strongly polluted areas, also indicated that those plants, moreover, had lower resistance to air pollution. However, differences within species in tolerance to edaphic conditions and to pollutants, as demonstrated in Table 4, are therefore of increasing importance and ought to be included in all tree-breeding work for the urban environment.

Table 4. Ecotype differences in *Sorbus aucuparia* to SO_2 (g dry weight). Håbjørg 1975.

Locality	Wild type	SO_2 resistant type
SO_2-exposed	2,2	4,3
Unexposed	3,5	3,4

Summary

This short review shows that the natural vegetation of Scandinavia is well adapted to the local climatic and edaphic conditions. It also shows that there is a great difference in adaptability within the species. Moreover, arctic and continental ecotypes seem to be poorly adapted to southern and maritime conditions, as, too, do southern ecotypes to arctic and continental conditions. Ecotypes from the fjord areas with a mixed selection pressure showed a wide adaptability. They could grow fairly well under maritime, arctic and continental conditions.

A possible change in the climate with increasing winter temperatures to above zero, may cause damage to the highly specialised arctic and continental ecotypes. The breeders of forestry, agricultural and horticultural crops should therefore take that into consideration in future breeding programmes.

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3 Species diversity, plant distribution and vegetation zones

Effects of climate change on species diversity and zonation in Sweden

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Introduction. Global warming from the increase in greenhouse gases has become a major scientific and political issue during the last decade. Estimates of present and future effects, however, have significant uncertainties. There have also recently been controversial claims that a global warming has been detected.

Results from most recent climatic models suggest that average global surface temperature will increase by some 1.5 to 6 °C during the next century, but future changes in greenhouse gas concentrations and feedback processes not properly accounted for in the models could produce greater or smaller increases. Forecast of the distribution of variables such as soil moisture or precipitation patterns have even greater uncertainties.

To make predictions about changes in species diversity and zonation on a regional scale, i.e. in Sweden, we should have information not only about the average temperature and precipitation but also the distribution of these variables during the year. Since the models are not yet good enough for these types of detailed forecasting, for the sake of the discussion we need to make some more or less probable assumptions:

- There will be an increase of greenhouse gases from now to 2050 equivalent to a doubling of carbon dioxide concentration.
- The average temperature in the north of Sweden will increase by 3-5 °C and in the south by 3-4 °C.
- Precipitation will increase by 10-30 %. Due to the higher temperatures the evaporation will increase too.

- The length of the vegetative growing period, number of days with an average temperature above 5 °C, is prolonged by 50 days.

These assumptions give a climate in the Stockholm region like we have today in the province of Scania. The inner part of Norrland will have the same climate as we have in the Stockholm region. In southern Sweden we will have a Mediterranean climate (cf. Figure 1).

Changed zonations. In Scandinavia it is primarily the length of the winter period which limits the distribution of various plant species. Locally the water deficiency is more important and also determines the formation of some vegetation types, for example sand heath, steppes (alvar vegetation), etc.

Even if the average climate is of great importance for the distribution of different species, extreme climatic events determine the survival not only of single individuals but also of whole populations.

Studies of climatic changes in the past have clearly shown how the vegetation zones have changed in time with the temperature in both north-south directions and upwards-downwards in the alpine area. Such displacements are going on also today. At the beginning of this century the average temperature was higher than during the last thousand years. As a consequence, the mountain coniferous forests were favoured and the timberline advanced over the open alpine areas and tundra. During the last decades there has been a remarkable deterioration in the climate of this region and there has been no seedling establishment at all, with the consequence that the timberline is moving downwards again.

Another important aspect is the human influence on vegetation zones through land use. Spruce plantations in the deciduous region and deciduous forests in central Sweden are some examples.

Some important effects of the climatic change in Sweden can be expected:

- The timberline will move upwards in the mountain areas and further north towards the Arctic Ocean. In the same way, the borderline between the southern and northern coniferous regions will move further north but with a delay of 75-150 years due to the life span of the trees. Oak (*Quercus* spp.), hazel (*Corylus avellana*) and elm (*Ulmus* sp.) will gradually become more common above the Limes Norrlandicus (see Table 1).

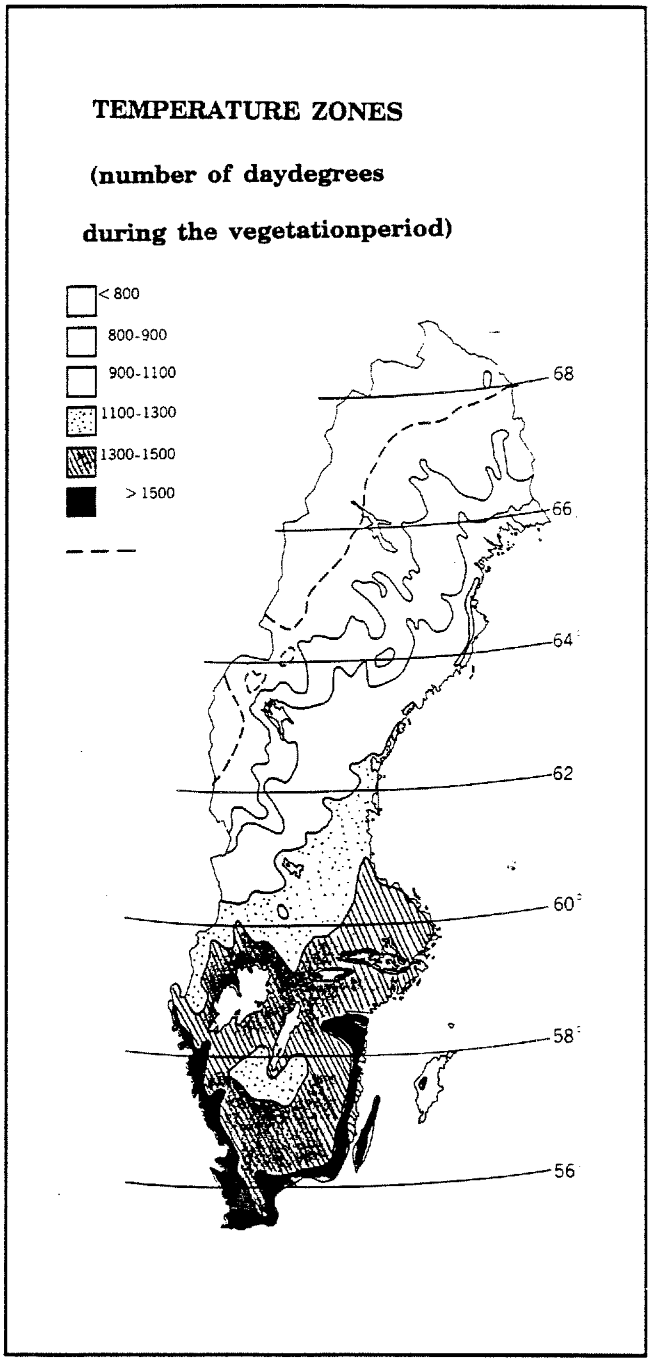

Figure 1 The current abiotic temperature zones in Sweden measured as number of day-degrees during the vegetative period.

- The alpine ecosystems, especially the subalpine and low alpine, will be influenced by increased competition pressure from immigrants. It is also probable that the limits will move upwards (Table 1).

- In southern Sweden the possibilities will be better for beech (*Fagus sylvatica*). Hornbeam (*Carpinus betulus*) will establish forests further north and at the same time Norway spruce (*Picea abies*) will move its western border eastwards.

- Several new tree species can be expected to immigrate from the continent, for example silver fir (*Abies alba*) and sycamore (*Acer pseudoplatanus*).

- The distribution pattern of many plant species will be affected. Most sensitive are of course those which have distribution limits in Sweden. In general, species with a southern distribution can be expected to advance further north. Examples are *Corylus avellana*, *Hedera helix* and herbs like *Galium odoratum*, *Hypericum tetrapterum*, *Mercurialis perennis* and *Orchis mascula*. Composites and sedges are expected to be especially favoured by a warmer climate. However, the land use during the last decades, especially in forestry, may have decreased their dispersal possibilities.

  On the other hand, species with a northern or eastern distribution can be expected to decline either for abiotic reasons or through competition. Examples are *Betula nana*, *Rubus arcticus*, *Lactuca alpina* and several alpine species (Table 1).

- It is difficult to speculate about effects on mires. Probably the water balance will change in different ways. A lowering of the water table in southern Sweden will increase the decomposition of organic material in the mires which will have an impact on existing bogs as well as the development of new ones.

- The ecosystems in southern Sweden are thought to be more vulnerable to water deficiency and drought stress, for example heaths and steppes. This may have an impact on the insect fauna.

- Salt marshes will be flooded by raising of the sea water table. This will have a temporary impact on the survival of salt marsh plant species. The importance of these biotopes for bird populations will also be affected.

- An increase in temperature can have negative effects on vegetation. Storm felling during winter is one example. The flowering of scots pine (*Pinus sylvestris*) is dependent on a chilling period and if the winter becomes warmer the natural rejuvenation will be cancelled out. The attack of pathogenes may increase, especially during winter.

- Soil formation processes are to a large degree determined by climate. In the northern part of Sweden it takes several hundred years for a podzol to develop. With increased temperature and precipitation the decomposition should increase and more nutrients will be available for the vegetation.

- During the last decade there has been a constant increase in nitrogen deposition and in southern Sweden today there are several areas which show symptoms of nitrogen saturation. With increased temperature and precipitation, especially during winter, nitrification and consequently nitrate leaching and acidification should increase. The release of nitrogen in the soil may also favour nitrophilous plant species, i.e. the nitrogen impact will be more obvious than today. Nettles (*Urtica* spp.), raspberry (*Rubus ideaus*) and cow parsley (*Anthriscus sylvestris*) are some examples of species which will be favoured.

The importance of rate of change. It is perhaps trivial that another climate in a defined region, warmer or cooler than today, will give another vegetation. The type of vegetation depends on the magnitude of climatic change. There may be doubt when or if a vegetation type of known composition will be established. Perhaps more important for the effects in a short term perspective, especially for the biological diversity, is the rate in change of climate. The projected climate changes will be much faster than the known changes since the last glaciation period.

The vegetation changes that will occur will be a result of an immigration - extinction process, i.e. a plant succession. Immigration is determined by establishment of seedlings of new species and extinction by death of the last adult individual of a species.

Table 1 Some characteristics of competitive, stress-tolerant and ruderal plants.

	Competitive	Stress-tolerant	Ruderal
(i) Morphology			
1. Life-forms	Herbs, shrubs and trees	Lichens, herbs, shrubs and trees	Herbs
2. Morphology of shoot	High dense canopy of leaves. Extensive lateral spread above and below ground	Extremely wide range of growth forms	Small stature, limited lateral spread
3. Leaf form	Robust, often mesomorphic	Often small or leathery, or needle-like	Various, often mesomorphic
(ii) Life-history			
4. Longevity of established phase	Long or relatively short	Long—very long	Very short
5. Longevity of leaves and roots	Relatively short	Long	Short
6. Leaf phenology	Well-defined peaks of leaf production coinciding with period(s) of maximum potential productivity	Evergreens, with various patterns of leaf production	Short phase of leaf production in period of high potential productivity
7. Phenology of flowering	Flowers produced after (or, more rarely, before) periods of maximum potential productivity	No general relationship between time of flowering and season	Flowers produced early in the life-history
8. Frequency of flowering	Established plants usually flower each year	Intermittent flowering over a long life-history	High frequency of flowering
9. Proportion of annual production devoted to seeds	Small	Small	Large
10. Perennation	Dormant buds and seeds	Stress-tolerant leaves and roots	Dormant seeds
11. Regenerative* strategies	V, S, W, B_s	V, B_T	S, W, B_s
(iii) Physiology			
12. Maximum potential relative growth-rate	Rapid	Slow	Rapid
13. Response to stress	Rapid morphogenetic responses (root—shoot ratio, leaf area, root surface area) maximising vegetative growth	Morphogenetic responses slow and small in magnitude	Rapid curtailment of vegetative growth, diversion of resources into flowering
14. Photosynthesis and uptake of mineral nutrients	Strongly seasonal, coinciding with long continuous period of vegetative growth	Opportunistic, often uncoupled from vegetative growth	Opportunistic, coinciding with vegetative growth
15. Acclimation of photosynthesis, mineral nutrition and tissue hardiness to seasonal change in temperature light and moisture supply	Weakly developed	Strongly developed	Weakly developed
16. Storage of photosynthate mineral nutrients	Most photosynthate and mineral nutrients are rapidly incorporated into vegetative structure but a proportion is stored and forms the capital for expansion of growth in the following growing season	Storage systems in leaves, stems and/or roots	Confined to seeds
(iv) Miscellaneous			
17. Litter	Copious, often persistent	Sparse, sometimes persistent	Sparse not usually persistent
18. Palatability to unspecialized herbivores	Various	Low	Various, often high

*Key to regenerative strategies (considered in detail in Chapter 5): V — vegetative expansion, S — seasonal regeneration in vegetation gaps, W — numerous small wind-dispersed seeds or spores, B_s — persistent seed bank, B_T — persistent seedling bank.

Normally, long-living plants are dominant in well established plant communities, i.e. K-species or competitive species (Table 1). This is relevant for the field layer also, many herbs having an average life span of 50-150 years. For many species, vegetamigration rates.

When the environment starts to change, many existing species cannot re-establish, but the adult individuals will keep their place for many years or decades. At the same time, seeds from new species can successively occupy the empty sites. These new species are either better adapted to the new environment or have a fast dispersal, i.e. r-species or ruderal species (Table 1).

The following can be expected:

- The diversity increases since immigration rate is higher than extinction rate in a qualitative sense. This means also that new species combinations, i.e. plant sociological units, will be established.
- In general the ecosystems will be more destabilized. The environment will be more unpredictable which means that species with a life strategy where more energy is allocated to reproduction than a long life, will be favoured. There will be **a change from competitive species towards more ruderal species.** This will also have an influence on several ecosystem variables.
- Due to the rate of change, several ecological relationships can be disturbed: host - parasite, plant - herbivore, predator - prey, etc.

Impact of climate change on flora and vegetation in Western Europe with special emphasis on the Netherlands

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Introduction. A global climate change is expected as a result of increased atmospheric CO_2 and other trace gases (the "greenhouse effect"). If there is a doubling of preindustrial CO_2 the global mean temperature will rise by 2 to 4.5 °C. This increase will be larger in the polar regions and less in the tropics, and will be larger in winter than in summer. A global intensification of the hydrological cycle (more precipitation and more evaporation) by 5-10 % is also expected. The most likely climate scenario for Europe is a rise in annual mean temperature that exceeds the rise in global, with uncertainty about rise in all seasons. A larger variability might initially result in decreasing winter temperatures. As far as precipitation patterns are concerned Europe, will follow the global tendency towards more precipitation and more evaporation. The period of precipitation deficit (in Western Europe, averages only a few month per year) could extend from summer to spring.

Prediction of climate change on a scale of for example the Netherlands cannot yet be made. A rise in temperature of 2 °C (not only in the annual mean but also in the seasonal mean, the greatest uncertainty in this being the winter temperature) is much larger than the actual differences within the Netherlands. If the actual differences are maintained the temperature in the southwest of the country will be more like that in northwest France or southern England. An intensification of the hydrological cycle by 10 %, more precipitation and more evaporation could result in a larger precipitation excess during winter and a larger deficit in spring and summer, if seasonal rainfall patterns remain the same. An increase in the length of the growing season will occur. The number of days increase will differ from region to region. For example, in the Netherlands the growing season will be lengthened by up to 30 days; for the Stockholm area this will be 40 days

(Ingelög 1986), for some parts of Norway even more than 100 days.

In France, the ecological conditions of SW France will be transferred into the Paris Basin; the ecological conditions of the latter to the Lorraine. An increase of 1 °C will transfer the climate of the Loire Valley into the Paris Basin (Ozenda & Borel 1987). Increase in precipitation will probably not counterbalance the greater dryness (reduction of water supply) produced by the warming, especially in the regions already affected by a rain deficit (i.e. Mediterranean).

Concerning the impact of the greenhouse effect on plant species, a distinction can be made between:
- direct effects as a result of increased CO_2
- indirect effects through climate change (temperature, precipitation, evaporation, etc.)
- from climate change, derived effects such as sea level rise, changes in sedimentation and erosion patterns, etc.

These effects can be synergetic or counteracting.

This paper will concentrate on the indirect effects, i.e. the impact of climate change on flora and vegetation. However, it should be borne in mind that climate is not the only factor which influences plant growth and distribution. Not a single climatic factor, but an interrelative complex set of variables, climatic as well as edaphic and biotic. The influence of a climate factor can be different for each stage of the life cycle of an individual plant species.

Changes in nature resulting from climate changes will take place at three levels:
1) Direct response of individual species to changing circumstances
2) Response of two or more organisms which naturally interact
3) Response of whole vegetations/ecosystems

Of course these levels are not strictly separate.

Level 1 Direct response of individual species

Phenological response. There are numerous examples of relations between climate factors (particularly temperature) and phenological features such as date of foliation, flowering, fruit setting.

Change in temperature will give rise to changes in the phenological features of a plant species, as was well illustrated by Erkamo for certain species in Finland during a warmer period early this century (Erkamo 1952).

Figure 1 gives flowering periods for a number of species in the Netherlands, based on 25 years of observation. An increase in temperature will shift these times earlier in the year. What the indications may be are difficult to grasp. With an earlier spring, winter rest of flower buds of e.g. fruit trees may be broken earlier; this might increase the vulnerability to frost damage (Landsberg 1981). Also disruption of relations between flowering and pollinators may occur.

Higher temperatures and a longer growing season should be particularly favourable for annual species, which have several life cycles per year (*Therophyta epiteia*). The number of life cycles may increase and thus lead to increase seed capital contributing to the weed problem, as many of these species are already aggressive weeds, such as *Stellaria media*, *Poa annua*, *Senecio vulgaris*, and *Lamium purpureum*.

On the other hand, certain short-lived species may have greater difficulty in setting seeds under extreme circumstances (e.g. drought). For perennials the situation is more complex, as they can often survive unfavourable periods vegetatively.

Warmer conditions and longer summers will promote a generally higher level of flower, seed and spore production.

Two phenomena which are particularly vulnerable to a temperature change are seed dormancy breaking by chilling and germination responses to temperature. In some arable weeds (e.g. *Chenopodium album*, *Polygonum aviculare*) requirements for chilling are allied to a need for subsequent exposure to light, or to higher temperature. These weeds form persistent seed banks, suggesting that the chilling requirement may be implicated, initially in delayed germination and seed burial, and subsequently in mechanisms of secondary dormancy, whereby germination of the buried seeds is favoured only by conditions obtaining in the early spring (Grime & Callaghan 1988). It can be expected that many arable weeds will germinate earlier in the season, adding to the weed problem. It has also been found that higher summer temperatures promote after-ripening in seeds of winter annuals, such as *Cardamine hirsuta*, *Erophila verna*, *Capsella bursa-pastoris* and *Stellaria media* (Baskin & Baskin 1986). Some summer annuals like

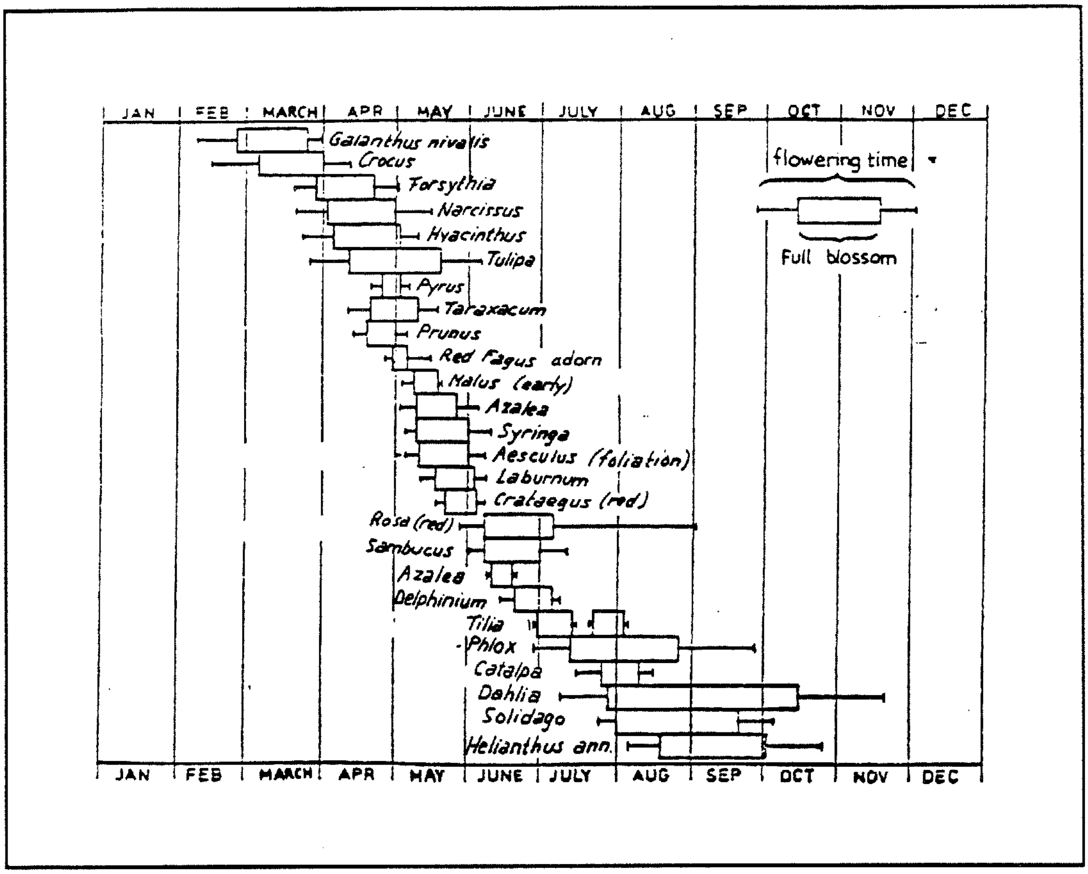


Figure 1 Average flowering period of plant species in De Bilt, central Netherlands, recorded over a period of 25 years. From year to year, flowering dates may shift two weeks earlier or later. In general flowering occurs in the same sequence each year (after Können 1983). An increase in temperature of 2 °C may shift flowering times by one month to the left.

Chenopodium album and *Amaranthus hybridus* at high temperatures rapidly gained the ability to germinate at high temperature, while usually requiring exposure to low temperature to after-ripen completely (Baskin & Baskin 1987). An expansion of these weedy species may be a result of climate change.

Adaptation. Adaptation to temperature change will take place by evolutionary adaptation, by acclimatisation and by changes in the distribution area.

Evolutionary adaptation (=genetic adaptation of the enzymatically determined tolerance range) is a slow process. It can be expected that annuals and species with great genetic variability will react by evolutionary adaptation sooner than long-living species.

Acclimatisation: within its genetic tolerance range the species can adapt its physiological tolerance when it is subjected to slow changes in its environment. Short-living species will probably respond quicker than perennials.

It can be expected that species with a broad ecological amplitude (e.g. euroec/eurytherm species) with a wide distribution will adapt easily, while species with a narrow amplitude (stenotherm species) will experience problems.

Changes in distribution. There are numerous examples of correlations between the occurrence of a species and one or more climate factors, e.g. snow cover, temperature; the distribution boundary takes a similar course as a certain isotherm (average min. or max. temp. or monthly isotherm, etc. see Grace 1987, Woodward 1987). This is not necessarily a direct causal relationship, but can also be a matter of reduction in the ability to compete (competitive power), as a result of changed physical environmental factors (Walter 1979).

At the limits of its distribution area a species often behave, differently from the centre of the area. It is less abundant, has other environmental requirements and different performance (including physiologically) (Haeck & Hengeveld 1979, Grace 1987, Hengeveld 1989).

Good temperature indicators are, for instance, *Ilex aquifolium* and *Hedera helix* for which both winter and summer temperatures are important in determining the ranges.

The east boundary of the range of *Ilex* is determined by the January isotherm of 0 °C; better still by a line demarcating where the maximum temperature is > 0 °C for at least 345 days per year (or the average temperature of the coldest month > -5 °C. In mid Holocene the species did not occur as far east, which might indicate colder winters. In the thermal maximum after the last Ice Age the species occurred much further north in Scandinavia than at present. Figure 2 illustrates, how *Ilex* may migrate northeastwards under a temperature rise, caused by doubling atmospheric CO_2.

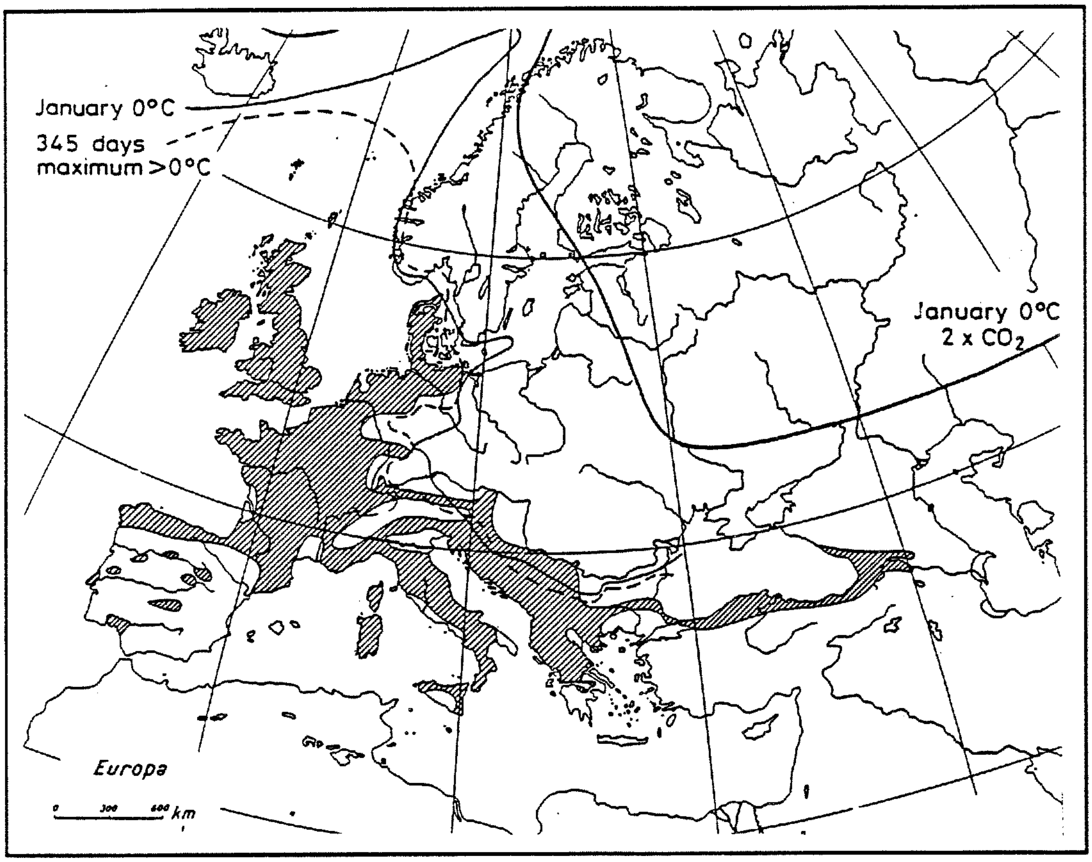


Figure 2 Present distribution of *Ilex aquifolium*. The eastern boundary coincides well with the January isotherm of 0 °C, even better with the line showing where the maximum temperature is above 0 °C for 345 days per year. The January isotherm of 0 °C under doubled CO_2 is also given, indicating the potential change in distribution of *Ilex* after climate change.

The distribution of *Hedera helix* is related to the temperature of the coldest month (-2 °C), as well as of the warmest month (ca. 13 °C); the less northern distribution being attributed to cooler summers. This species will probably expand further north into Scandinavia, where it has been before in warmer times (Ingelög 1986). Many examples are known from palynological research of species which have declined or increased because of climate changes, e.g. *Pinus silvestris* at a marginal site in Sweden slowly declined during the Little Ice Age (1300-1850); because of a change in temperature the regenerative capacity declined and there was high mortality amongst young trees (Kullman 1987).

In the Netherlands and the adjacent part of NW Germany and in parts of England the summers will become somewhat continental (higher temperatures, dryness), the winter on the other hand more atlantic (warmer and humid). It is to be expected that plants with a northern distribution (boreal and boreal-montane elements) which have southern outposts will retreat. This is likely to be the case with *Empetrum nigrum* (southern limit halfway across eastern Netherlands), *Trientalis europaea*, *Linnaea borealis* and *Arnica montana*.

Expansion of ranges (expanding within their present area as well as expanding their present borders) may be expected of species with higher temperature requirements and a (sub)mediterranean or mediterranean/atlantic distribution and probably also some subcontinental species which may migrate via river valleys (predominantly the Rhine, see Jongman 1989). Species with high temperature requirements, and also species which are more eurytherm, may be favoured at places where they occur under suboptimal conditions.

Species with high temperature requirements are for instance C4 species which are adapted to warm and dry conditions, predominantly occurring in the tropics and subtropics, with increasing occurrence in the temperate zone. It is very likely that they will be favoured by climate change.

At present there are 21 C4 species naturalised in the Netherlands, some are already spreading rapidly; 60 C4 species are recorded as casuals (Van Voorst 1984). Some of these C4 species are considered as the worst weeds in the world, e.g. *Cynodon dactylon*, *Echinochloea crus-galli*, *Portulaca oleracea* and *Cyperus esculentus*, some *Amaranthus* spp. (Holm et al. 1977). The occurrence of C4 plants is related to temperature and human activities. For monocotyles the temperature limit of min. temp. of 8 °C is given; for dicotyles also plus the availability of water. They have a short life cycle and profit from resistance to certain herbicides and late germination. With higher spring temperatures, early and increased germination may be expected.

Table 1 gives a tentative list of plants which are expanding or are inclined to do so in the Netherlands and/or Belgium (see De Langhe et al. 1983; Heukels & Van der Meiden 1983; Van Kampen 1989; E. Weeda, Rijksherbarium, pers. comm.). Temperature and continentality values are given according to Ellenberg (1979) or Landolt (1977). Unfortunately these values are not exactly comparable, as Ellenberg's values apply to plants with the core of their range in western Central Europe and Landolt's to species occurring in Switzerland only. For some plants no indicator values could be found; they are not considered as being naturalised in these areas. Life form is also given.

The most striking feature is that a large number of species with a mediterranean/submediterranean (south European) or subcontinental distribution, are now expanding from southwest in a northerly (northeasterly or somewhat northwesterly) direction, a feature which is precisely what may be expected as a logical adaptation to climate change. Many of the species show high temperature indicator values (7 according to Ellenberg; 4 or 5 from Landolt; species from warm places).

Several of the species are therophytes or pioneers and known from more ruderal open sites (various Gramineae). Therefore, further spread of many of these species may be enhanced by a gradual temperature increase.

It should be emphasised that human activities such as eutrophication and increasingly disruptive effects on vegetation (intensive agriculture, urbanisation, deforestation, dereliction and recreational pressure, creation of open spaces) have lead in the recent past to the explosive spread of many weedy species in Western Europe.

The ability of a species to expand its area depends on its mobility, i.e. its dispersal capacity and its migration rate, as well as the accessibility of the new area. Rare species with specific environmental requirements may not be able to effectively migrate, even when climate change may favour reproduction and vigour. Other species may be too slow to migrate to new suitable habitats.

Level 2 Interaction between 2 species

Because each species has a different ecological relationship to climate, climate change will elicit an immediate and individualistic response from each species, thus altering the competitive balance among species in a vegetation. What the outcome may be of these changes in competitive power is difficult to

Table 1 Preliminary list of species which are spreading in the Netherlands and/or Belgium and surrounding areas. The distribution of these species may be enhanced by a temperature increase. L = life form; T, K & N = indicator values according to Ellenberg or Landolt (italics): T = temperature, K = continentality and N = nitrogen; F = neophyte; W = weedy. See also footnote.

Family:	Species:	L	T	K	N	F	W	Remarks:
	C_4-species:							
Amaranthaceae	Amaranthus blitoides	t	7	7	7	x	x	alien
	Amaranthus retroflexus	t	9	7	9	x	x	N Amer., subcosm.
Portulacaceae	Portulaca oleracea	t	8	3	7	x	x	trop.
Cyperaceae	Cyperus esculentus	g	-	-	-	x	x	trop.
	Cyperus fuscus	t	6	4	4	-	-	
Gramineae	Cynodon dactylon	g,h	7	3	5	x	x	subcosm.
	Digitaria ischmaenum	t	6	4	3	x	x	temperate
	Digitaria sanguinalis	t	7	3	3	x	x	subcosm.
	Echinochloa crus-galli	t	7	5	4	x	x	
	Eragrostis minor	t	7	5	4	x	x	trop., warm-temp.
	Eragrostis pilosa	t	7	3	?	x	x	trop., warm-temp.
	Setaria glauca	t	7	4	6	x	x	subcosm., warm-temp.
	Sorghum halepense	t	-	-	-	x	x	S Eur., trop.
	C_3-species:							
Chenopodiaceae	Chenopodium botrys	t	9	2	6	x	x	med., S Eur.
Urticaceae	Parietaria judaica	h	7	2	7	-	-	S/SW Eur.
	Parietaria officinalis	h	7	4	7	-	-	C & S Eur.
Papaveraceae	Corydalis claviculata	t	6	1	?	-	-	W Eur., atl.
	Fumaria muralis	t	-	-	-	-	-	S & W Eur., ruderal
Cruciferae	Cardaminopsis arenosa	h,c	X	4	3	-	-	N & C Eur, ruderal
	Cardaria draba	h,g	7	7	4	x	-	S & C Eur.
	Coronopus didymus	t	*4*	*2*	*4*	x	x	alien
	Descuriania sophia	t	6	7	6	x	x	ruderal
	Diplotaxis tenuifolia	c,h	7	3	4	-	x	S, W & C Eur., ruderal
	Rapistrum rugosum	t	*4*	*2*	*4*	x	x	S Eur., ruderal
	Sisymbrium austriacum	h,t	7	5	7	x	x	SW & C Eur.
Resedaceae	Reseda luteola	tb	7	3	3	-	-	S, W & C Eur., ruderal
Papilionaceae	Medicago arabica	t	-	-	-	x	x	S/SW Eur.
	Medicago minima	t	7	3	1	x	x	S Eur.
Euphorbiaceae	Mercurialis perennis	h,c	5	3	7	-	-	S & C Eur.
Lythraceae	Lythrum hyssopifolia	t	7	5	3	-	-	subcont.
Umbelliferae	Oenanthe crocata	h,g	5	2	3	-	-	SW Eur.
	Falcaria vulgaris	h	7	6	3	-	-	Med./S Eur
Balsaminaceae	Impatiens glandulifera	t	7	2	7	x	x	alien, ruderal
	Impatiens balfouri	t	*5*	*3*	*4*	x	-	alien
Malvaceae	Abutilon theophrasti	t	*5*	*3*	*4*	x	x	alien
Gentianaceae	Blackstonia perfoliata	t	7	3	4	-	-	W Eur., atl.
Scrophulariaceae	Linaria repens	h	*4*	*4*	*4*	-	-	SW Eur., ruderal
	Linaria supina	c	*4*	*4*	*2*	-	-	
	Parentucellia viscosa	t	-	-	-	x	-	S/SW Eur
	Veronica peregrina	t	*4*	*2*	*4*	x	x	alien
Orobanchaceae	Lathraea clandistina	g	-	-	-	-	-	SW Eur.

Plantaginaceae	Plantago arenaria	t	7	5	4	x	x	E, S & C Eur
Compositae	Crepis vesicaria	t	5	3	4	-	-	W & S Eur.
	Filago vulgaris	t	7	3	2	-	-	W, C & S Eur.
	Gnaphalium luteo-album	t	6	5	3	-	-	subcosm.
	Inula conyza	h	6	2	3	-	-	(C) Eur., N Afr.
	Lactuca serriola	t	7	7	4	-	x	S & W Eur., ruderal
	Lagoseris sancta	t	-	-	-	-	-	Med./SE Eur.
	Picris hieracoides	h	-	5	4	-	-	W, C & S Eur.
	Picris echioides	t	5	2	4	x	-	Med./S Eur
	Pulicaria dysenterica	h	6	3	5	-	-	
	Senecio inequidens	h	-	-	-	x	x	alien, ruderal
	Tragopogon dubius	h	5	3	4	x	x	ruderal
	Xanthium strumarium	t	7	5	6	x	-	S Eur., ruderal
Gramineae	Chenopodium botrys	t	9	2	6	x	x	Med
	Parietaria judaica	h	7	2	7	-	-	(fluv. dun.)
	Parietaria officinalis	h	7	4	7	-	-	(fluv. dun.)
	Bromus rigidus	t	5	3	2	-	x	ruderal
	Mibora minima	t	5	2	2	-	-	S/SW Eur.
	Nardurus maritimus	t	-	-	-	-	-	S/SW Eur.
	Poa bulbosa	h	8	7	1	-	x	S & C Eur.
	Vulpia fasciculata	t	-	-	-	-	-	Med., S Eur.
	Vulpia ciliata	t	5	2	3	x	-	S/SW Eur., Med.
	Vulpia myuros	t	5	3	3	-	-	S Eur., subcosm.

Footnote

L	C	*Herbacecus chamaephyte*, herb with buds above the ground
	H	*Hemicryptophyte*, buds near the ground
	G	*Geophyte*, buds within the soil, often with storing organs
	T	*Therophyte*, short living "annual" plant

Ellenberg 1979

T	5	moderate warm climate
	6	*intermediate*
	7	mostly in *warm* climate (more or less rare in northern Central Europe)
	8	*intermediate*
	9	only in very *warm* climate (mediterranean)

K	1	*euoceanic*, reaching Central Europe only in the extreme west
	2	*oceanic*
	3	between 2 and 4
	4	*suboceanic*, main area in whole Central Europe
	5	*intermediate*, from suboceanic to subcontinental
	6	*subcontinental*, main area in eastern Central Europe
	7	between 6 and 8

N	1	only in soils *very poor* in mineral nitrogen
	3	mostly in *poor* soils
	5	mostly in *intermediate* soils
	7	mostly in soils *rich* in mineral nitrogen
	8	*nitrogen indicator*
	9	only in soils *very rich* in mineral nitrogen (indicating pollution, manure deposits or similars)

Landolt 1977

T 4: Plants occurring chiefly in the colline region in summy places also higher. Plants widely distributed in the lower regions of Central Europe.
5: Plants occurring only in the warmest situations. Plants chiefly found in Southern Europe.

K 2: Plants occurring chiefly in regions with sub-oceanic climate; they cannot stand late frosts or great extremes of temperature.
3: Plants occurring chiefly outside extreme continental regions. Found almost everywhere in the region.
4: Plants occurring chiefly in regions with relatively continental climate; capable of withstanding extremes of temperature, low winter temperatures and slight air humidity; not found in places where the snow lies for long periods.

N 2: Plants occurring chiefly on poor soils; usually not found on rich to over rich soils, or not able to compete there. Indicators of poor soil.
3: Plants occurring chiefly on medium poor soil to medium rich soil; neither found on very poor soil nor on over fertilized soils.
4: Plants occurring chiefly on rich soils, hardly found on poor soils. Indicators of rich supply of nutrients.
5: Plants occurring chiefly on soils with over-rich supply of nutrients (usually nitrogen); never found on poor soil. Indicators of over fertilization, in water, indicators of pollution.

foresee. It may have immediate impact on the competition between crops and weeds, where C3 weeds may compete over C4 crops or vice versa.

Other interactions are plant/pathogen and plant/animal. Pests and diseases may be enhanced by climate change, such as rusts in wheat, outbreaks of which are related to certain temperature levels.

Level 3 Response of natural vegetation

The global distribution of the main vegetation zones of the world as well as altitudinal zonation are predominantly determined by rainfall and temperature (Holdridge 1967, Walter 1979). Change in climate will induce changes in these zonation patterns.

Several analogies can be mentioned. During the climate optimum in the Holocene (6500 BP) temperature was 2-3 °C higher; the northern limit of the boreal zone was situated 200-300 km further north. In the Alps the treeline and snow line were situated about 400 m higher; in England and Scotland 200-300 m. During the warmer period of the Middle Ages, the treeline in northern England lay about 150-200 m higher (Ford 1982).

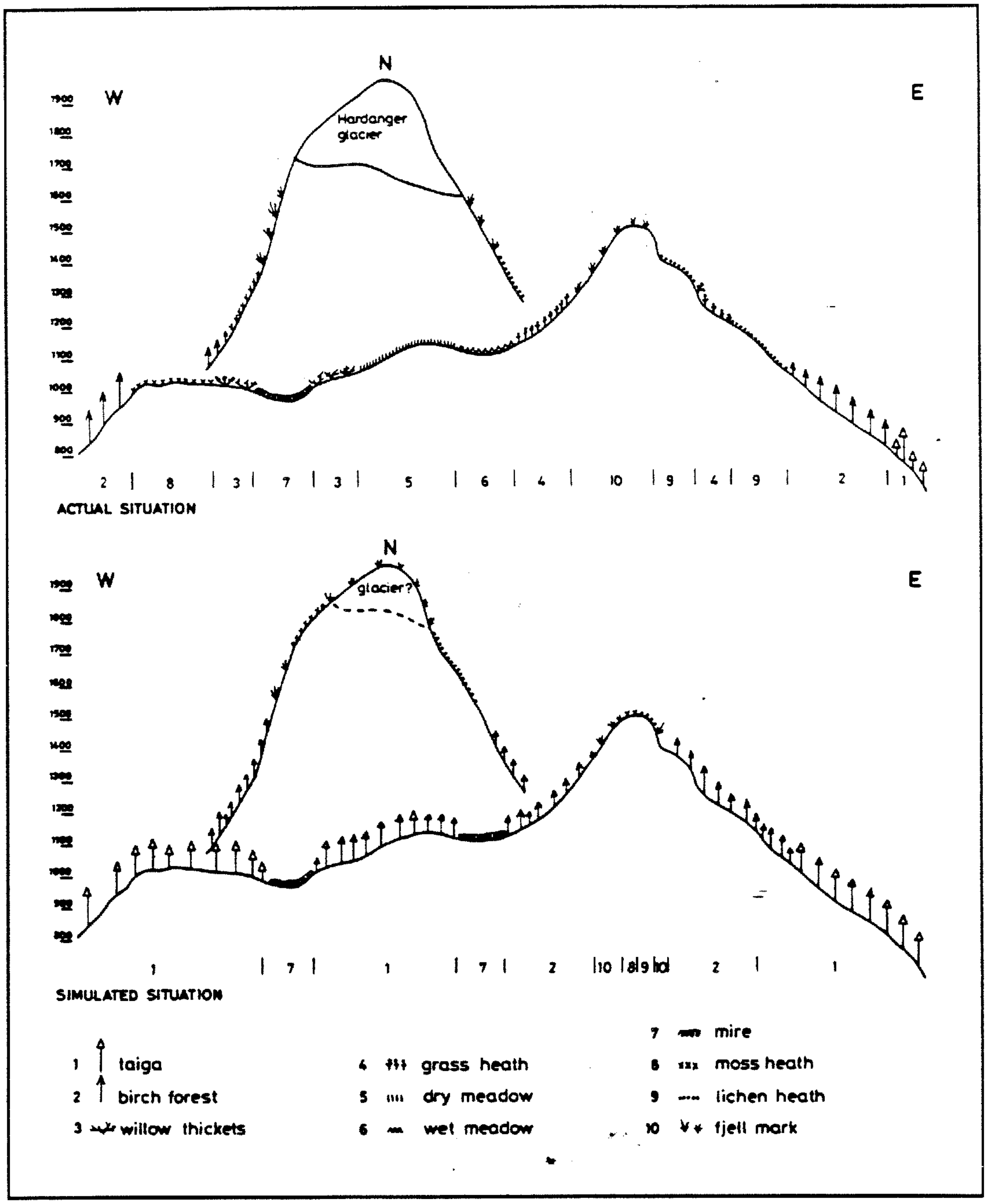
An increase of 2-4 °C would mean an altitudinal shift of vegetation zones of up to 700 m. Many plant species will be bound to disappear as they will not find their suitable habitat any longer (see Figure 2 in Peters & Darling 1985).

Simulation studies by Emanuel et al. (1985) and De Groot (1988) show potential shifts in the major vegetation zones. The largest alterations would take place in the tundra and boreal forest zones. The tundra may disappear almost completely and be changed to a taiga-like vegetation with birch and conifers, comparable to the present taiga. The boreal forest zone may change to another forest type adapted to a cool temperate climate or change into steppe, depending on precipitation.

Van Huis & Ketner (1987), in a study about climate sensitivity of natural ecosystems, looked at the possible vegetation changes in various national parks in Europe, using the GISS climate scenario (Hansen et al. 1984, Bach 1986) to simulate new local climates. For Scandinavia, the Hardangervidda was taken as the example.

Figure 3 shows the hypothetical vegetational changes which may occur in this area, assuming the following climate changes:

Figure 3 Schematic cross section of the vegetation zonation (hypothetical situation) on the Hardangervidda plateau, under present climatic conditions and under simulated conditions after doubling the CO_2 content of the atmosphere (for details see Van Huis & Ketner, 1987).



- * On the mountain plateau at 1000 m a.s.l. a warmer climate will not rule out the frost period and the probability of extreme weather conditions. The frost period will be shortened by 2 months from the end of November until the beginning of April, but there will be more snow.
- * Important are the higher mean summer temperatures together with the rise in the number of days above 10 °C to 50, allowing tree growth.
- * A strong increase in precipitation from 730 mm to almost 1000 mm annually with weak peak

values (80-100 mm) in midsummer and in early winter.

The precipitation in winter can be expected as snow, resulting in a snow cover that is thicker than the present-day one.

- Evaporation will not increase parallel to the increased precipitation under the new conditions (i.e. humid climate). The result will be surplus water; more runoff can be expected, with consequences for the regional hydrological conditions. The effects will be most pronounced in late winter and spring.

A comparable present-day climate is found on the western mountain slope and fjord coast around Trondheim (127 m a.s.l.).

Figure 4 gives the degree of impact of climate change in natural ecosystems in Europe. For the details see Van Huis & Ketner 1987.

Discussion. These studies are all very conjectural and speculative, and whether all such changes will take place remains to be seen. However, if the predictions about climate changes are correct then this climate change is already taking place and nature is reacting to it, although this is still not observable. There is no abrupt climate change nor an abrupt response from nature.

There are many factors which cause changes in the range of species. Changes in the occurrence of species take place continuously. It will therefore be difficult to single out climate change as the driving force (Van Kampen 1989). However, the conclusion of Grime & Callaghan (1988) that "The current land-use policies are conducive to rapid floristic response to climate change and will encourage invasion by thermophilous species (also aliens) with a "weedy" (i.e. fast-growing and fecund) character" is to be taken seriously, as is illustrated in the above.

So far nothing has been said about the time-span over which these possible changes may take place. It is impossible to make any prediction. One reaction pattern may occur within some decennia (change in distribution area), while the other requires a longer time scale (change of total vegetation composition). Because of the rate at which climate change is going to take place (doubling of CO_2 in the next 50-100 years), a normal gradual course in the processes of adaptation, acclimatisation and natural migration is less likely, considering the life-spans of many species such as trees.

Lags in the response of the vegetation to climate change can occur for many reasons, e.g.

- Effective geographical dispersal barriers, such as open water, high mountain ranges, highly exploited areas such as large agricultural areas.
- Poor accessibility because of unfavourable edaphic conditions. Will a deciduous forest be able to establish on the wet, acid, taiga soils? Or will a mediterranean vegetation from a calcareous soil be able to move to northern soils which predominantly are humic and acid? "Mismatches" will occur and species will be hampered in their migration.
- Low adaptability to additionally changed environmental factors, such as day-length.
- Competition from resident plants that continue to occupy space under the changed climate conditions.
- Direct and indirect effects of atmospheric pollution, e.g. accumulation of nitrogenous deposits in the soil. At higher temperatures, N availability will be enhanced. This process limits plant establishment and will be favourable for nitrophilous species with a more ruderal character.
- Ecotypic variation within the range of a species.
- Inadequate dispersal capacity and migration rate.

Relatively little is known about migration rates of plant species. From palynological studies, Davis (1986) has shown that Norway spruce (*Picea abies*) 9000 yrs ago migrated at a rate of 200 km per century; other tree species migrated far more slowly (10-40 km per century). The predicted temperature increase of 2-4 °C in mean temperature over the next 50 years corresponds to a shift of up to 350 km in the boundary of a species range. If species are to remain in areas with equitable climate they have to migrate at rates of the order of 1 m/hour (Soulé, cited in Dobson et al. 1989).

Changes in flora and vegetation in the coming 50 years will therefore probably not be as large as climate change would allow, because of a high number of retarding factors. An immediate response i.e. an alteration in the competitive balance among species in the vegetation, will occur; some species will spread rapidly into new areas, others may not and may decrease in occurrence. The whole competition process in a community itself may take many

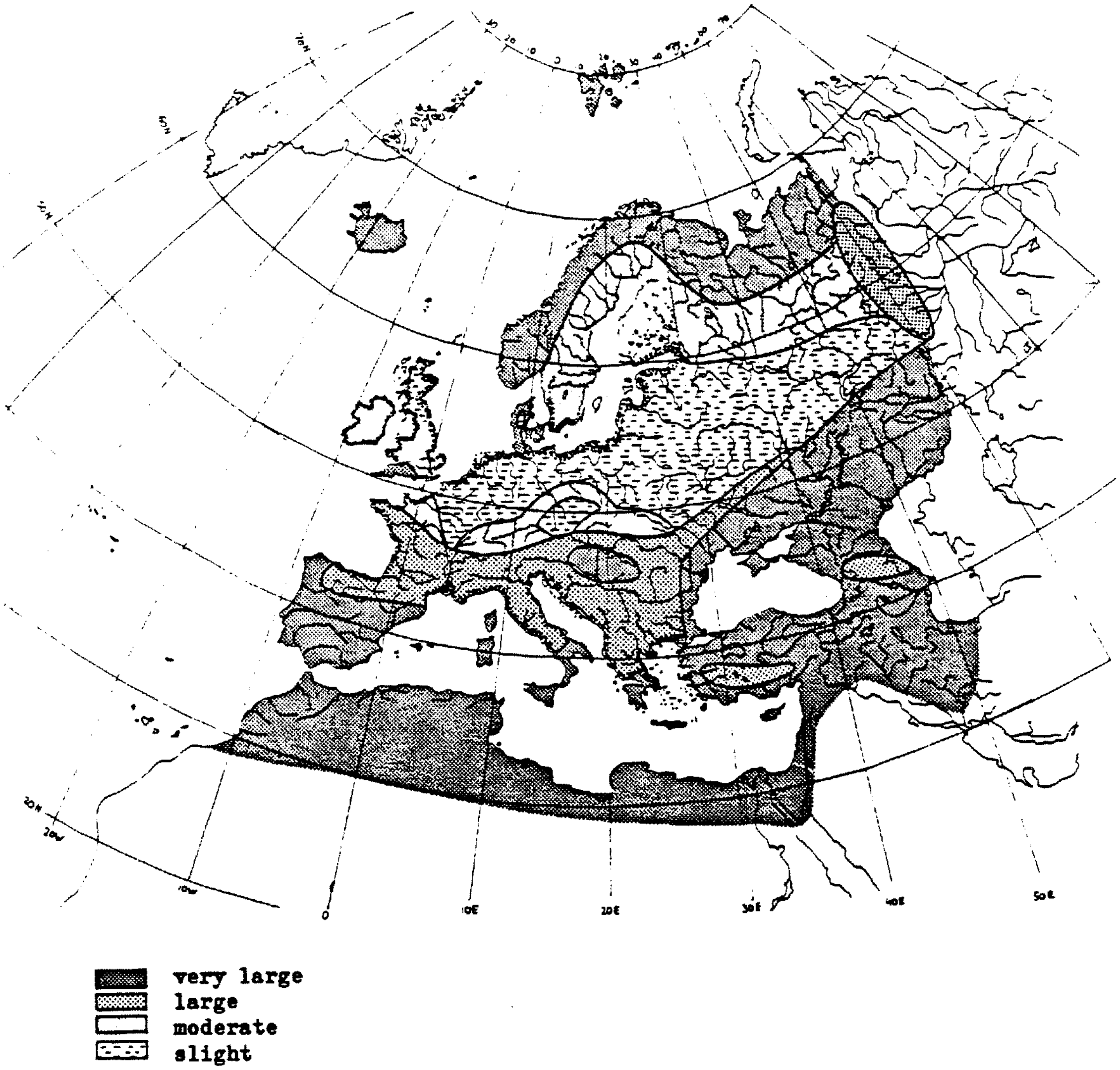


Figure 4 Schematic representation of the impact of climate change on natural ecosystems in Europe (after van Huis & Ketner 1987).

decades to work through into a visible changed natural vegetation (cf. Ingelög 1986).

Extreme climate events may enhance certain developments, e.g. catastrophic die-back of forests caused by drought or frost.

In vegetation types which are continuously under human influence (as is the case with many plant communities in highly agricultural countries) changes may be visible sooner than in natural stable vegetation such as climax forest (see also Van Huis & Ketner 1987).

Vegetation is spatially and temporally non-static. Changes take place continuously. There are external and internal fluctuations but a striving towards a dynamic equilibrium.

If atmospheric CO_2 has doubled and if climate has changed as predicted, then we still have to bear in mind that there will be no equilibrium situation in the natural environment.

An equilibrium will only be obtained if external factors remain relatively constant over a long period of time, fluctuating around a long-term mean.

Research needs

- Phenological research:
    - analysing older phenological data
    - phenology of species within their range over a temperature gradient
    - what is known about phenological behaviour during extreme climatic events?
- Studies on explosive invasion of species, including aliens.
- Population research of certain species along a climate gradient.
- Migration studies at the boundary of the range of a species.
  Is a threshold value the cause of that boundary?
- Studies on isolated populations of the same species; in what way have ecotypes evolved?
- Temperature requirements for germination; periodicity of seed bank in relation to temperature.
- Dispersal strategies and dispersal rates.
- Impact of corridors (ecological infrastructure) on dispersal of plants.

Conclusions

- There will be an individualistic dynamic response by plant species to climate change, in growth as well as in distribution.
- Each species will have its own rate and direction of migration from its present habitat.
- Direction of migration will be determined by the presence of competitors, local environmental conditions and human activities.
- The ability to compete, i.e. competitive power determined by e.g. a complex of environmental factors and surrounding species, will change.
- Some species may be too slow to react and will be limited in distribution or become extinct.
- Other species may vanish because suitable habitats are no longer available or cannot be reached.
- Thermophilous species will be favoured by temperature increase, C4 species may have an advantage over C3 species; fast-growing and fecund species will be favoured.
  Many of these types of species are weedy species, thus contributing to a weedification of NW Europe.
- Present land-use policies will add to this weedification problem.
- New species combinations - new vegetation types - will appear.
- The magnitude of the impact will be strongly dependent on geographical location, habitat type, lag times and the way in which a system will be able to adapt to new circumstances. A temperate climax forest may experience fewer big changes than for instance an alpine grassland.

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Predicted floristic change and shift of vegetation zones in a coast-inland transect in Central Norway

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Presuppositions for the effect scenario

In 1978-84, the vertical distribution and habitats of 150 taxa, 91 vascular plants, 34 mosses, 8 hepatics and 17 lichens, were mapped in a coast-inland transect in Central Norway (Figure 1). Hypotheses concerning limiting factors for the distribution of species were put forward. It was suggested that the major climatic factors determining the distribution patterns are summer temperature, winter temperature and humidity. In this context, the emphasis is put on summer and winter temperatures, due to the very uncertain rainfall scenarios.

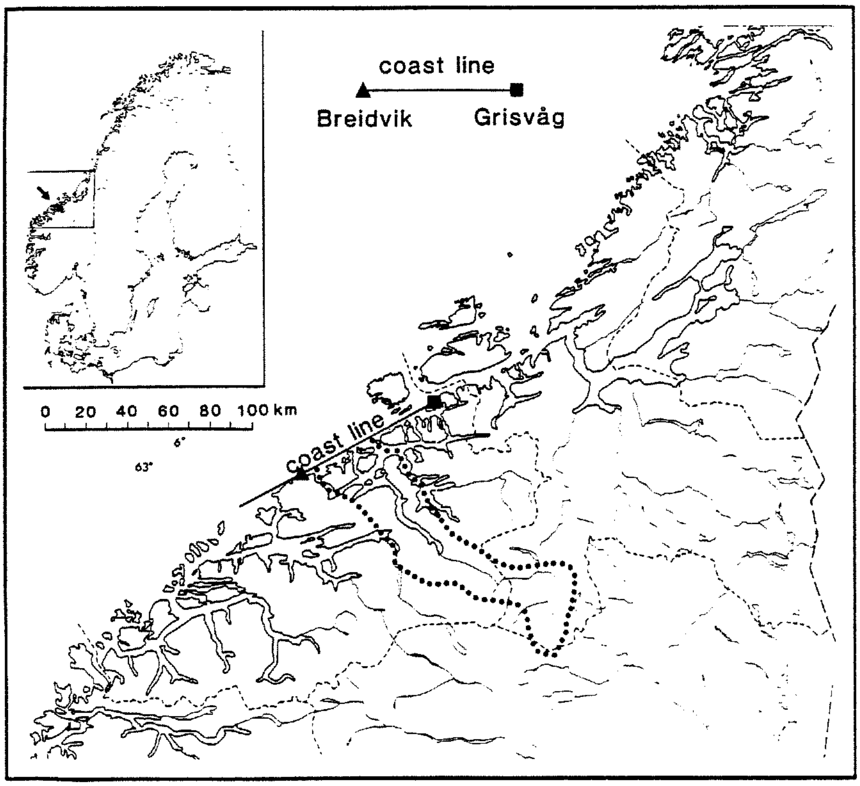
The taxa mapped in the work of Holten (1986) were grouped into four main types of vertical distribution based on the factors suggested.

The coast-inland transect has very steep temperature, moisture and elevation gradients that sharply define the western, eastern, upper and lower limits of species. The transect is found to be very well suited for studies of the cause/effect relationship between climatic factors and plant distribution. In addition, steep gradients are convenient for the study of ecotones and migration of species when research and monitoring programmes on the ecological effects of climatic change are being carried out.

Climate scenario for Norway

The climate scenario used in the present effect scenario has been worked out by a group of Norwegian climatologists (see Grammeltvedt, this volume) during the winter of 1990. The generally accepted temperature scenario for a 2 x CO_2 atmosphere is:

Figure 1 The location of the area investigated.



- mean temperature increase for December, January and February ca 4 °C
- mean temperature increase for June, July and August ca 2 °C.

Rainfall will also show a general increase - 5 to 15 % spread through the year depending on distance from the coast and time of year. The prediction that ground moisture will increase during winter and decrease during summer is thought to be of great ecological significance, at least for the position of western and eastern limits of continental (xerophilous) and oceanic (humidiphilous) plant species (see below).

For the specific coast-inland transect in Central Norway we have made a simple prediction of the temperature trend through the year, based on monthly mean temperatures (Figures 2a and 2b). The oceanic station of Kristiansund has a gentle temperature curve, indicating a high degree of thermic oceanicity. The predicted 2 x CO_2 curve indicates still higher thermic oceanicity for Kristiansund (Figure 2a). Using a base temperature for growth of 6 °C, the growing season in Kristiansund will be extended by 110 days, that is to 303 days. Since 6 °C is probably a relatively high base temperature, the growing season in coastal areas of Western and Central Norway will be 365 days. Using the same reasoning for Hjerkinn, the growing season would be extended by only 36 days in the new climate, due to the much steeper temperature curves at continental stations. The extension of the growing season in the fjord and valley districts will be intermediate between the 36 days at Hjerkinn and the 110 days at Kristiansund.

The warmer climate will certainly have great consequences for the distribution of snow in winter. The changed position of the zero degree isotherm (see Figure 3) will give a rough indication of the new "snow limit". No doubt the position of this "snow limit" will have great significance for ecology, and therefore for the distribution of plants and, through them, animals. The predicted temperature scenario for Norway will result in snow-free mountains up to about 700-900 m above sea level in coastal and fjord districts, not taking into account the very uncertain rainfall scenario.

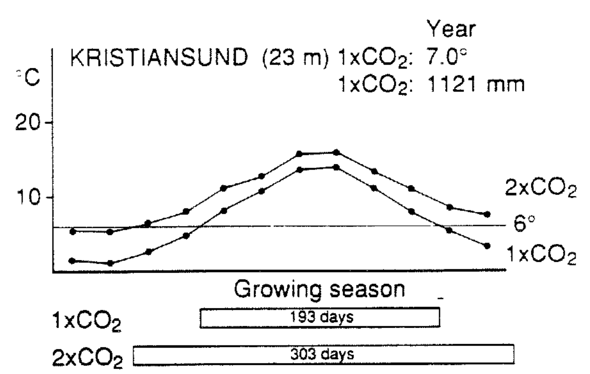


Figure 2a The yearly trend of monthly mean temperatures at present and under the 2 x CO_2 scenario for the oceanic Kristiansund station. The growing season indicated by the horizontal bar being extended by 110 days under the 2 x CO_2 scenario.

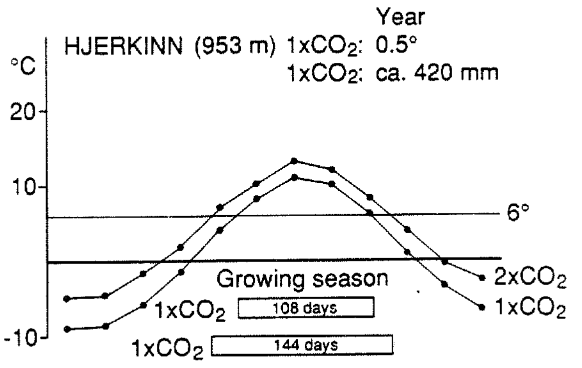
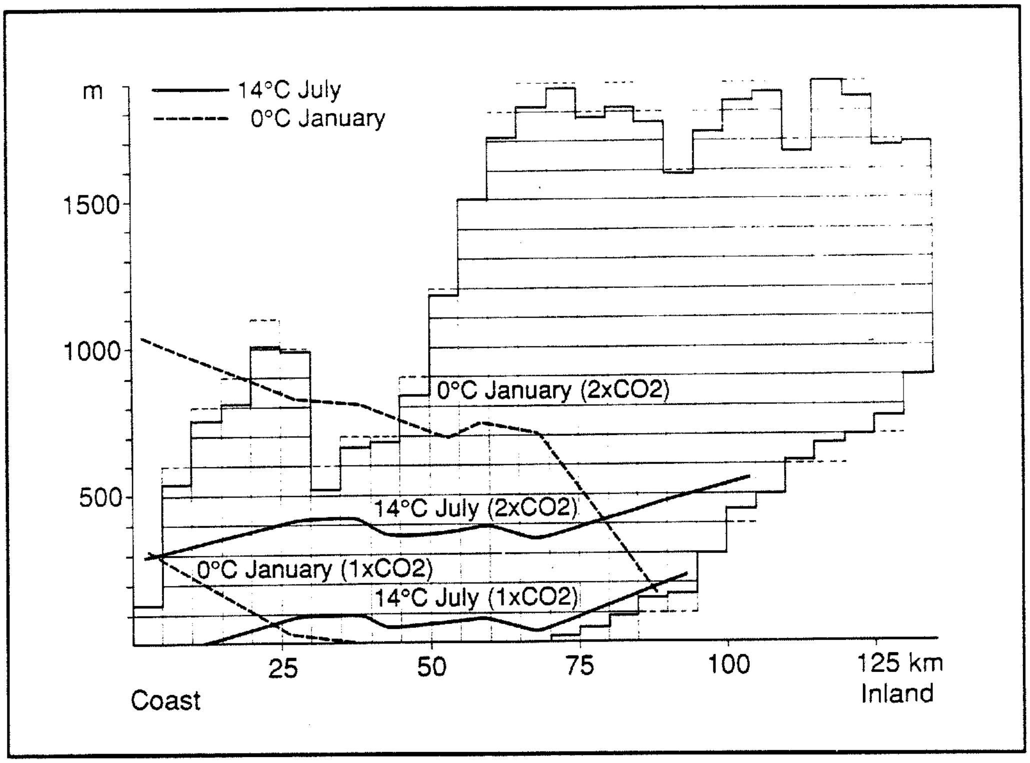


Figure 2b The yearly trend of monthly mean temperatures at present and under the 2 x CO_2 cenario for the continental Hjerkinn station. The growing season indicated by the horizontal bar being extended by 36 days under the 2 x CO_2 scenario.

Figure 3 The positions of the 14 °C isotherm for July and the 0 °C isotherm for January, under current conditions and under the Norwegian 2 x CO_2 climate scenario.



Hypotheses for explaining vertical plant distribution

The good correlation between vertical distribution patterns and climatic parameters (Holten 1986) has led to the following hypotheses and predictions regarding the vertical distribution of species and plant communities in a warmer Central Norway.

Basic hypotheses for general plant distribution in the coast-inland transect are:
- **low winter temperatures** are the main limiting factor towards inland for frost-sensitive plants (good correlation between eastern distribution limits (frost limits) and the position of January isotherms has been documented),
- **high winter temperatures** are an important limiting factor for some continental species that avoid coastal areas with mild winters (good correlation between western distribution limits and position of January isotherms has been documented),
- **low summer temperatures** are the main limiting factor towards higher elevations for more or less thermophilous plants (good correlation between upper limits (ripening limits) and the position of July isotherms has been documented),
- **low humidity** (low hygric oceanicity) is the main limiting factor for humidiphilous plant species (hygrophytes) towards inland and the lowlands (good correlation between eastern distribution limits and the position of precipitation isohyets has been documented),
- **high humidity** (high hygric oceanicity) is an important limiting factor for xerophilous and continental plant species towards the more humid coastal areas (good correlation between western distribution limits and the position of precipitation isohyets has been documented).

The high degree of coincidence between distribution limits and limiting ecological factors is schematically illustrated in Figure 4 and defines 6 main types of distribution:
- **thermic oceanicity** (winter temperatures) defines the eastern limits of frost-sensitive coastal plants and the western limits of eastern plants that avoid areas with mild winters ("southwest coast avoiders" (Dahl 1951),
- **summer temperature** (high temperature demands) defines the upper limits of thermophilous (warmth-demanding) lowland plants and probably the lower limits of some mountain plants,

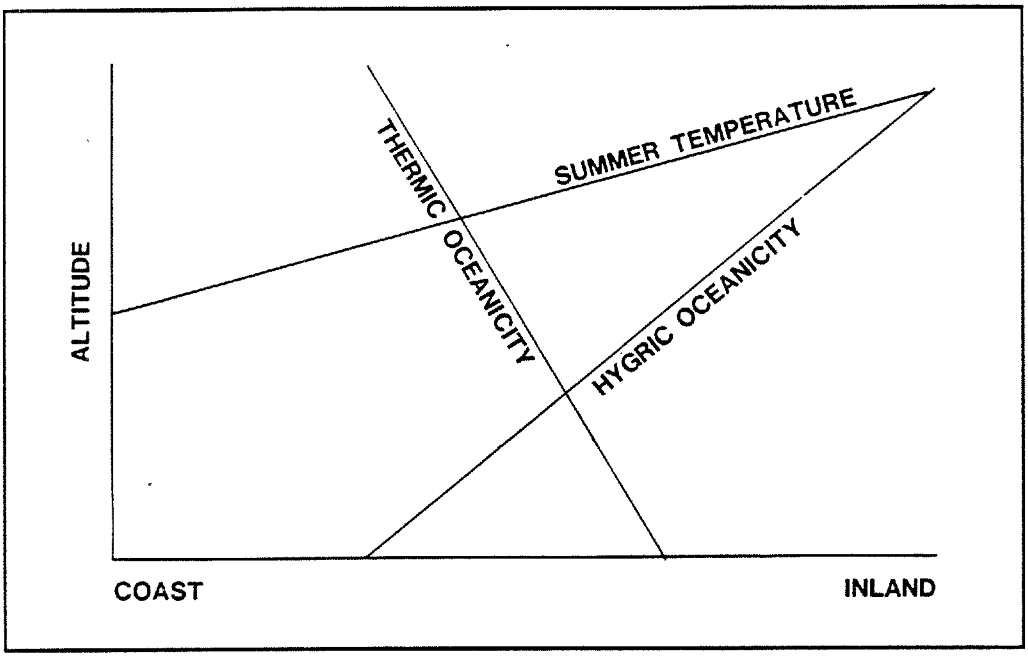


Figure 4 A schematical representation of the main ecological factors limiting plant distribution in the coast-inland transect.

- **hygric oceanicity** (humidity) defines the eastern limits (and sometimes the lower limits) of humidiphilous coastal plants and the western limits of continental and xerophilous plants.

The prediction below about plant distribution under the Norwegian climate scenario (see Grammeltvedt, this volume) is based on the hypotheses above. In addition, it is suggested that the predicted change in climate will not lead to ecosystem collapse, including the extensive death of species and communities. Instead, the main response in the ecosystem will be a change in interspecific competition leading to changes in the floristic composition of plant communities.

The response in species groups to climatic change

The response of plants to climatic change is specific for the individual species. Four main types of response can be distinguished:

- increase
- decrease
- existence threatened (extinction)
- no change

Frost-sensitive species (winter-thermophilous species). The predicted increase in winter temperature of 4 °C will certainly greatly influence thermic oceanicity (see Figure 3), and therefore some frost-sensitive coastal vascular plants in the transect. For the coastal station of Kristiansund this will result in a January mean temperature of 5-6 °C, comparable with central parts of England today. Using the displacement of January isotherms from Figure 3 and the hypothesis for the limitation of frost-sensitive plants (see above), we are able to predict **the potential distribution.** Comment: We may call this method **correlative modelling** of species distribution in relation to climatic change, as it is based on a more or less good correlation between isotherms or isohyets and distribution limits.

It is predicted that the following frost-sensitive plants (see Figure 5) will expand eastwards along the fjords in Central Norway and to higher levels (the approximate limiting January isotherm towards colder areas is indicated in °C):

Ilex aquifolium	1
Chrysosplenium oppositifolium	0.5
Asplenium adiantum-nigrum	0.5
Dryopteris borreri	0.5

Sedum anglicum	0
Lonicera periclymenum	0
Primula vulgaris	0
Carex binervis	-1
Hyperium pulchrum (Figure 5)	-1
Conopodium majus	-2
Polygala serpyllifolia	-2.5
Digitalis purpurea	-3
Luzula sylvatica	-4

The prediction indicated in Figure 5 is of course a simplification as we have not considered such factors as topography, geology, interspecific competition, etc.

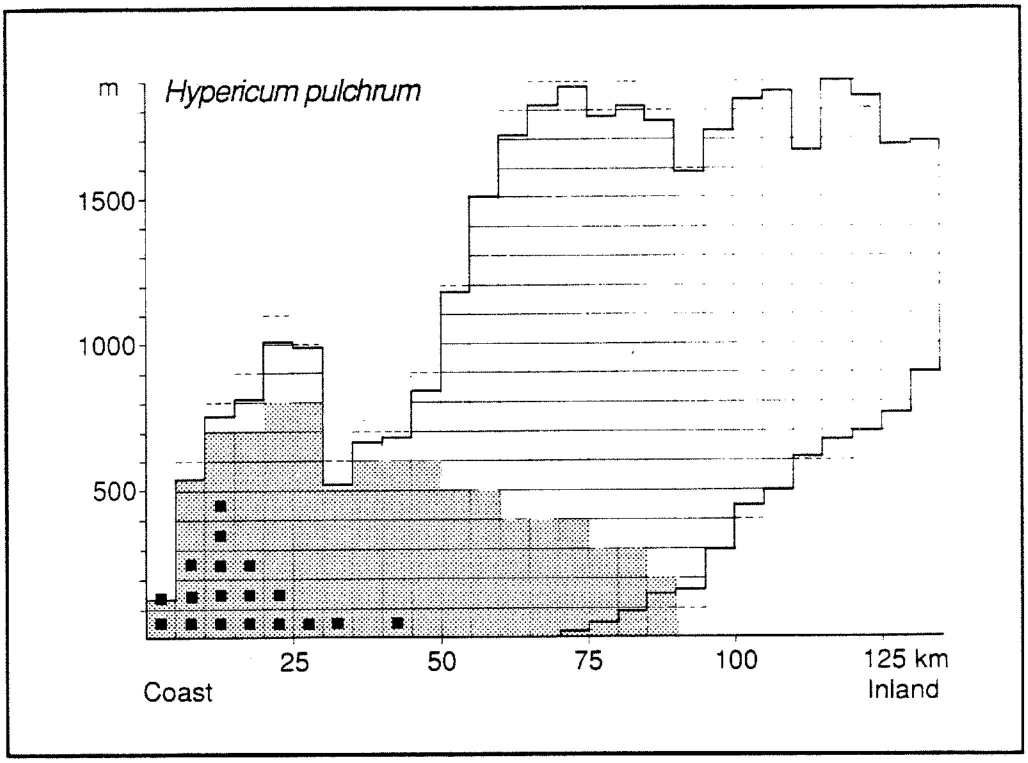


Figure 5 Present (= mapped) (dots) and predicted (shaded area) vertical distribution of frost-sensitive species in the coast-inland transect from Kristiansund to the main watershed on the Dovre mountain plateau. Vertical axis: height a.s.l. Horizontal axis: distance from the coast (after Holten 1986).

Eastern and northeastern species (southwest coast avoiding species). Many eastern and northeastern plant species have a distribution that is complementary to that of the frost-sensitive plants, and it is suggested that they have the opposite response to changes in thermic oceanicity (here expressed as January mean temperatures). The eastern and northeastern plants in Norway have their main distribution areas in northeast Europe or even in some cases Siberia. These plant species demand a **"real winter rest"**, that is, in the autumn their stalks wither entirely and the plant has no physiological activity. The underlying physiological mechanism explaining the lack of eastern and northeastern plants in the winter-mild districts of West Europe is not very well known. However, good correlations between their western distribution limits and the trend of January isotherms have been shown (Dahl 1951, Holten 1986, Salvesen 1988, 1989). In Scandinavia, at least in Sweden and east of the main watershed in Norway, the eastern and northeastern species group is rich in species, especially in boreal coniferous and subalpine birch forest, boreal mires and arctic/alpine areas (see below). The role played in the vegetation by these more or less continental plant species rapidly decreases west of the main watershed in Norway. The most important tree species in Scandinavia, Norway spruce (*Picea abies*), belongs to this group, although it has no natural occurrences in the coast-inland transect. The most important southwest coast avoiders (see Figures 6 and 7) in the transect are listed below (see also Holten 1988, Salvesen 1988, 1989) (the approximate limiting January isotherm towards winter-mild areas is indicated in °C):

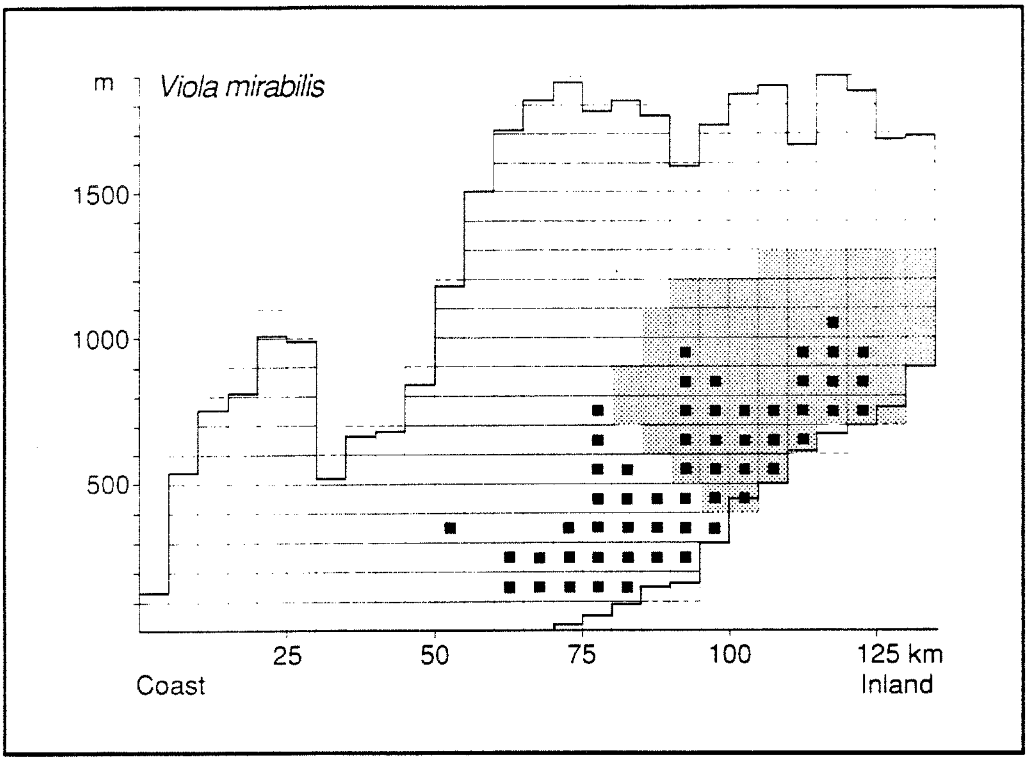


Figure 6 Present (= mapped) (dots) and predicted (shaded area) vertical distribution of a southwest coast avoiding species (eastern species) in the coast-inland transect (after Holten 1986).

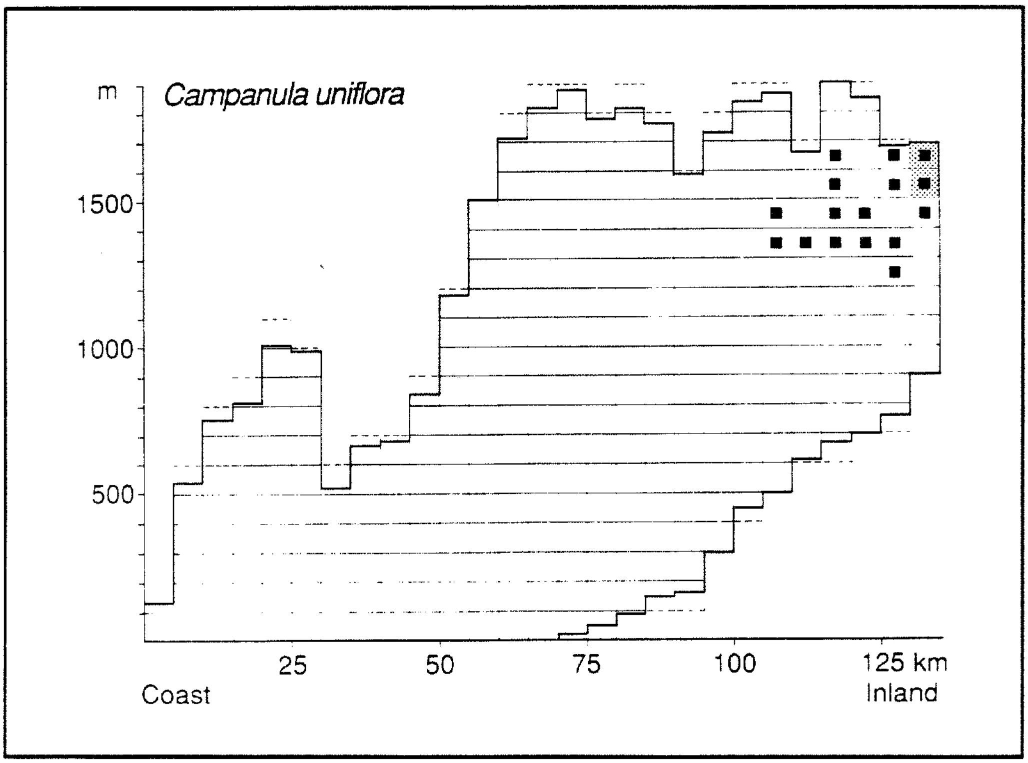


Figure 7 Present (= mapped) (dots) and predicted (shaded area) vertical distribution of a southwest coast avoiding mountain species in the coast-inland transect.

Carex heleonastes	-12
Carex capitata	-10
Carex aquatilis	-7
Epilobium davuricum	-6
Botrychium boreale	-6
Petasites frigidus	-6
Salix starkeana	-6
Carex vesicaria	-6
Polemonium caeruleum	-5
Poa remota	-2
Carex buxbaumii	-1
Scirpus hudsonianus	-1
Viola mirabilis (Figure 6)	-1
Arabis glabra	-1
Aconitum septentrionale	-1
Viola biflora	-1
Calamagrostis stricta s.l.	0
Goodyera repens	0
Moneses uniflora	0
Scheuchzeria palustris	0
Corydalis intermedia	0
Carex digitata	0
Hypericum hirsutum	0
Lathyrus vernus	0.5
Pyrola chlorantha	0.5
Gagea lutea	0.5
Actaea spicata	1

It is predicted that the western limits of the above species will show a general retreat eastwards in the transect. Some of the species may have to retreat east of the main watershed to find a sufficiently low thermic oceanicity for their existence, for example *Carex heleonastes* and *Carex capitata.*

Humidiphilous coastal species (hygric oceanic species). The dampness of air and soil depends on the relationship between precipitation and evapotranspiration at a specific site. The rainfall scenario (Eliassen & Grammeltvedt 1990) shows a 5-15 % increase in rainfall, depending on the region and the time of year. The growing season is likely to receive an increase in rainfall of about 10 %, according to DNMI and NILU. However, due to the increase in both summer and winter temperatures, increased evapotranspiration will largely compensate for this. The net result will probably be drier soil conditions in the growing season, including a lower water table in most places.

The preliminary snow cover scenario shows a longer season without snow, up to 85 days shorter winter for the simulated west Norwegian climate (N.R. Sælthun, pers. comm.). This is consistent with predicted extension of the growing season in continental areas (Figure 2b). The response which the humidiphilous coastal plants will show to the changed humidity is somewhat uncertain. The most typical humidiphilous coastal plants, belonging to oligotrophic mire, heath and forest vegetation in western and central parts of the transect are (approximate limiting yearly rainfall isohyet towards the drier continental areas indicated in mm):

Cornus suecica	700
Narthecium ossifragum	800
Blechnum spicant	800
Thelypteris limbosperma	900
Scirpus cespitosus ssp. germanicus	1100
Erica tetralix	1300
Pedicularis sylvatica	1400

The lower limits of humidiphilous coastal plants will probably retreat in the lowlands of inner districts of the transect, because shorter winters and therefore little or no snow protection in winter will result in increasing exposure to occasional frosty periods and to drying out at their lower and eastern limits.

Xerophilous eastern (continental) species (xerophytes). The western and in some cases the upper limits of xerophilous and continental plant species are determined by excessive humidity, (here expressed as annual rainfall), just as the eastern and sometimes lower limits of humidiphilous coastal plants are determined by too low humidity. Hence, many xerophilous species are complementary to many humidiphilous ones. The most extreme xerophilous vascular plant species in the transect, in decreasing degree of xerophili downwards in the table, are (approximate limiting rainfall isohyet towards wetter areas indicated in mm):

Androsace septentrionalis	600
Carex ericetorum	600
Thalictrum simplex	600
Ranunculus polyanthemus	600
Viola rupestris	700
Dianthus deltoides	700
Carex ornithopoda	800
Pulsatila vernalis	800
Heracleum sibiricum spp. sibiricum	900
Plantago media	900
Acinos arvensis	900
Cotoneaster integerrimus	1000
Viscaria vulgaris	1000
Carex muricata	1200
Festuca ovina	1200

The probable response of xerophilous plants is that they will increase and expand westwards and towards higher levels, due to the predicted decrease in soil dampness in the growing season and shorter winters.

Thermophilous species (warmth-demanding species). The distribution of thermophilous species (lowland species) is complementary to that of mountain plants. The summer temperature scenario (ca 2 °C increase) indicates a general expansion of this plant group. The most common thermophilous species with upper and northern limits in the hemiboreal or southern boreal zones in Scandinavia, but also occurring in the coast-inland transect, are listed below, arranged according to decreasing temperature demands downwards (see Figures 10, 12, and 13):

Rubus nessensis
Cephalanthera longifolia
Quercus robur
Torilis japonica
Alliaria petiolata
Luzula campestris
Festuca gigantea
Carex sylvatica
Bromus benekenii
Brachypodium sylvaticum
Epipactis helleborine
Sorbus rupicola
Allium ursinum
Geranium lucidum
Alnus glutinosa
Fraxinus excelsior
Lathyrus niger
Frangula alnus
Crataegus monogyna
Verbascum thapsus
Verbascum nigrum
Sanicula europaea
Ulmus glabra
Ranunculus ficaria
Viburnum opulus
Corylus avellana
Clinopodium vulgare

The general expansion of thermophilous plant communities and southern vegetation zones northwards is indicated on the map of "Potential vegetation regions for Norway" (Holten 1990b).

Mountain plants and northern plants. Part of our mountain flora has a genetically continental constitution. Hence, such plants may belong to the group of southwest coast avoiders, being absent or infrequent on coastal mountains, where thermic oceanicity is too high for them. If this hypothesis, that they avoid coastal areas due to too high winter temperatures, is valid, many mountain plants will experience this as an additional stress factor to episodes of high summer temperatures (Dahl 1951, Gauslaa 1984). Many edaphically demanding and fairly continental mountain plants whose optimum is in the Dovrefjell area, Central Norway, have a western limit in the transect that correlates well with the trend of January isotherms, indicating thet they are southwest coast avoiders (see Figure 7) (approximate limiting January isotherms towards areas with mild winters are shown in °C):

Sagina cespitosa	-12
Campanula uniflora (Figure 7)	-11
Draba alpina	-10
Luzula arctica	-10
Minuartia rubella	-10
Poa artica s.l.	-10
Poa stricta	-10
Ranunculus nivalis	-10
Stellaria crassipes	-10
Vahlodea atropurpurea	-9
Sagina intermedia	-9
Phippsia algida	-9
Draba oxycarpa	-9
Luzula parviflora	-9
Silene uralensis	-9
Carex parallela	-8
Chamorchis alpina	-8
Minuartia stricta	-8
Oxytropis lapponica	-7
Draba fladnizensis	-7
Gentianella tenella	-7
Kobresia myosuroides	-7
Artemisia norvegica	-6
Astragalus frigidus (see Holten 1990a, p.26)	-6
Poa flexuosa	-5
Astragalus norvegicus	-5
Salix arbuscula	-5
Carex microglochin	-4
Carex misandra	-4
Carex atrofusca	-3
Carex adelostoma	-2
Carex atrata	-2
Carex saxatilis	-2
Salix myrsinites	-2
Pedicularis oederi	-2
Saxifraga cespitosa	-2
Juncus castaneus	-1

I suggest that species in the list above that have a limiting January isotherm of -10 °C or lower belong to a group of plants that is really threatened if winter temperatures are going to increase by about 4 °C. The most threatened ones are those having a typical middle alpine distribution, that is, they occur today only above about 1400 m on Dovrefjell, Central Norway. This level may also be the approximate potential new timberline. In addition to the importance of winter temperature for the western delimitation of southwest coast avoiding mountain plants, **summer temperature** and **humidity** are no doubt important for the lower limit of many mountain plant species in Scandinavia (see Dahl 1951). Therefore both the lower and western limits will be affected by the climate scenario.

The response of plant communities

With regard to limiting factors we can use the same reasoning for plant communities as for the species. We may also apply the concept of complementary plant communities to the vertical occurrence of communities in the transect. I suggest that the group of plant communities belonging to the order *Quercetalia robori-petraeae* (= atlantic oak forests in a wide sense) is rather demanding as regards winter temperature (see Figure 8). The floristic similarity between certain coniferous forests and acid oak forests is relatively high. However, in oak forests (mainly *Quercus robur*) we find a group of rather frost-sensitive species, the most important being *Hypericum pulchrum*, *Lonicera periclymenum* and *Holcus mollis*.

It is predicted that the oak forests (Figure 8) will expand eastwards along the fjords and to higher levels in the transect, whereas the western limit of many southwest coast avoiding species, many of which have their optimum occurrence in tall herb communities belonging to the order Adenostyletalia, will in general retreat eastwards and upwards (Figure 9). The frost-sensitive and southwest coast avoiding communities are in this respect complementary.

We may expect a floristic change from dominating tall herbs to dominating tall ferns for the westernmost tall herb stands indicated (mapped) in Figure 9, towards stands with *Athyrium filix-femina* for the southern boreal and middle boreal zones, and towards stands dominated by *Athyrium distentifolium* for the northern boreal and low alpine zones (cf. Holten 1990).

It is predicted that in the transect tall herb communities with *Aconitum septentrionale* will rarely form stands below about 600 m. However, although the time vegetation requires to respond is very difficult to foresee, much more than 50 years is surely needed to establish a climax vegetation because the potential tall fern vegetation will of course need to both migrate and establish itself following the potential death of *Aconitum septentrionale*. As regards the oak forests (Figure 8), the migration of the Oak (*Quercus robur*) itself will be quite slow, perhaps depending largely on physical transport of acorns by red squirrels (*Sciurus vulgaris*), jays (*Garrulus glandarius*) and other birds and animals that forage on acorns.

The thermophilous forests, mainly *Ulmus glabra* and *Corylus* forests, are expected to expand their distribution eastwards and upwards in the transect (Figure 10) and in Norway as a whole (see the map of potential vegetation regions for Norway, Holten 1990). The potential uppermost stands of *Ulmus glabra* and *Corylus avellana* in the transect, will be at about 800 m in the Oppdal-Drivdalen area. The new species limits for *Ulmus* and *Corylus* will be at 900-1000 m a.s.l. It is predicted that *Ulmus* will be the most effective migrator of the two species, and may during the course of some decades be able to invade the neighbouring low herb birch forests on steep south-facing slopes in Central Norway. Such low herb sites close to the current *Ulmus* and *Corylus* stands should therefore be ideal sites for monitoring vegetation change (permanent plots) including registering the processes of migration, establishment and growth.

The thermophilous plant communities with *Ulmus glabra* and *Corylus avellana* will probably invade north-facing slopes below 300-400 m in the fjord and valley districts, today inhabited by mesotrophic *Betula* and *Alnus incana* forests. The complementary plant communities to the thermophilous lowland communities are the mountain plant communities. When temperatures are elevated, followed by timberlines elevating, the pure mountain plant species and communities will retreat. This effect scenario is indicated in Figure 11 for the upper boreal/low alpine bilberry heaths. It is predicted that the bilberry (*Vaccinium myrtillus*) itself will decline at its current lower limit because of strong competition from the more thermophilous lowland herbs.

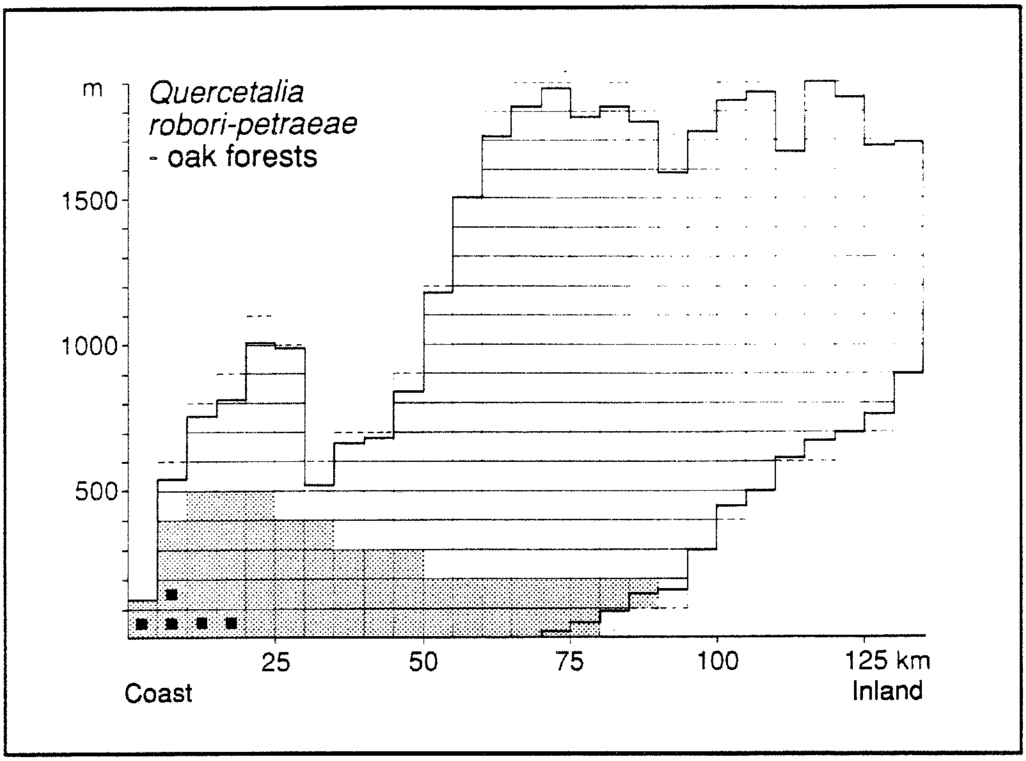


Figure 8 The expansion of atlantic oak forests belonging to the order *Quercetali robori-petraeae.*

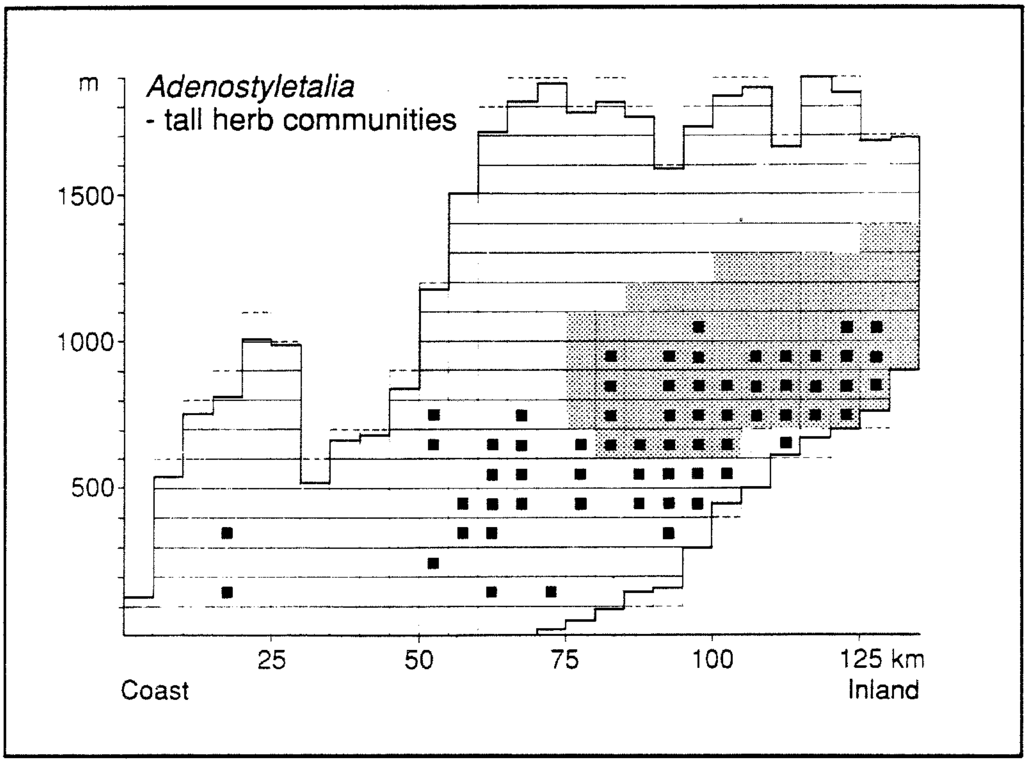


Figure 9 The retreat of south-west coast avoiding plant communities belonging to the order *Adenostyletalia.*

Figure 10 The expansion of thermophilous plant communities ("noble deciduous forests") belonging to the order *Fagetalia sylvaticae*.

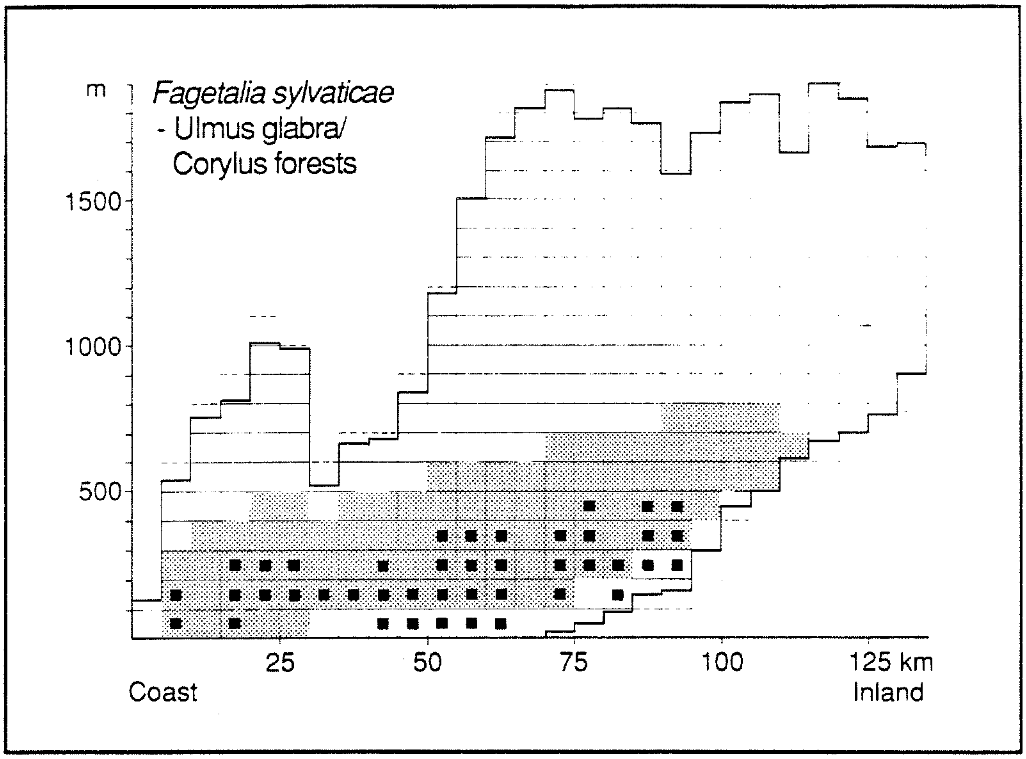
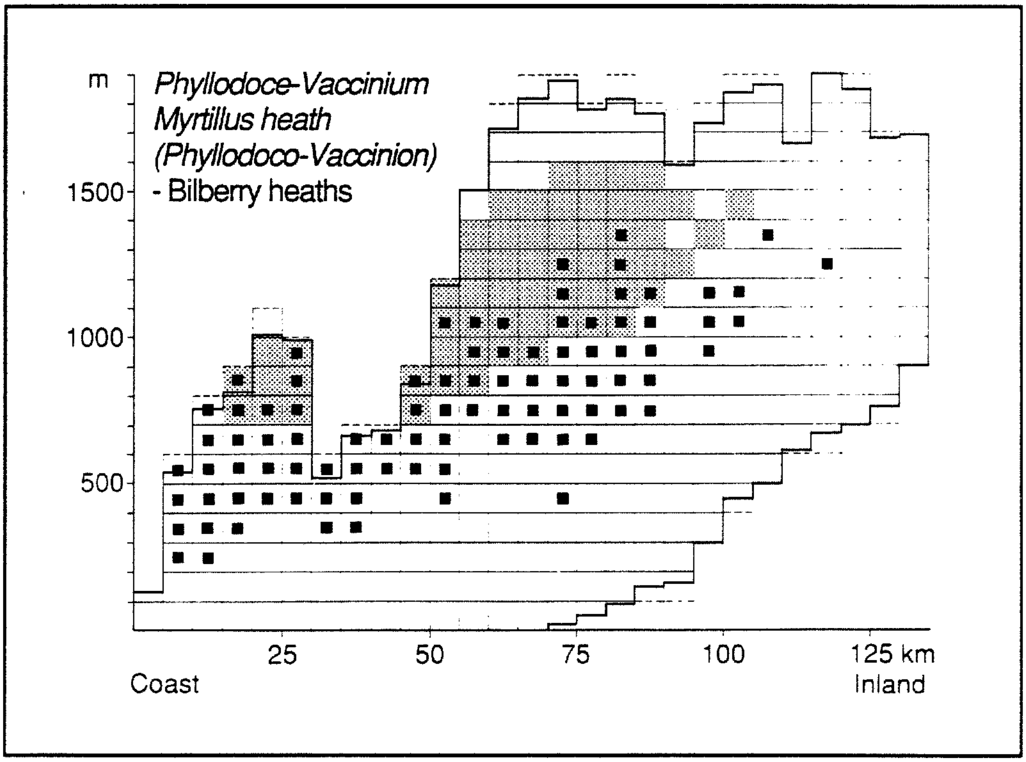


Figure 11 The predicted elevation of bilberry heaths in a wide sense belonging to *Phyllodoco-Vaccinion*.



Shorter winters, giving very little snow protection for *Vaccinium myrtillus* and drier soils in summer, will lead to more xeric conditions in the eastern part of the transect, resulting in a possible succession from *Vaccinium myrtillus* heaths to *Festuca ovina* grass heaths.

Effects on vertical zonation of vegetation

A prediction is made for the whole of Norway for horizontal vegetation zonation based on the climate scenario made by Eliassen & Grammeltvedt (1990). Since the map of vegetation regions (= zones) (Holten 1990b) did not take into consideration the rate of change, migration barriers, etc., the vegetation zones are only potential. The map shows a large quantitative change in the zones, especially for the warmer lowland zones and the alpine zones. For Norway as a whole, it is predicted that the temperate (= nemoral) zone will increase from 0.7 to 12.8 % of the total land area. The hemiboreal, southern and middle boreal zones will increase less. The northern boreal zone (= mountain forests, mainly with *Betula pubescens*) will be reduced to about a quarter of its current area, from 29.9 to 8.4 %. Almost the same retreat is predicted for the alpine zone, with a reduction from 29.6 to 7.1 % (see Holten 1990a). This prediction is supported by the general principle that a relatively small elevation of the timberline results in a large reduction of the bare alpine area. The potential forested area of Norway is predicted to increase from the current 66 % to about 88 % under the 2 x CO_2 scenario. (Comment: We all know that the real forested area in Norway today is far below 66 %, due to such factors as lack of superficial deposits, agriculture, urbanization, etc.).

Qualitative vegetation changes involve death of plant species, migration and establishment. All this need tens or hundreds of years, at least the migration process which is hampered in many ways. For instance, the thermophilous lowland species on their migration northwards across the flat countryside of South Scandinavia and the North European Plains will in principle meet three kinds of **migration barriers**: 1. cultivated land, 2. open sea, fjords and rivers, and 3. mountains. If the predicted rate of climatic change is extremely rapid, the existence of many thermophilous plant species will be threatened, not directly by the new climate, but by interspecific competition from other species which are better adapted to the new climatic conditions.

Migration of species is no doubt much easier in hilly or mountainous country. This is the case in the coast-inland transect in Central Norway. On steep slopes there is a short distance between vegetation zones, and the predicted increase in summer temperature of 2 °C may result in the *Betula* timberline being elevated about 300 m in the continental part of the transect. Along a slope inclining 30° this corresponds to a displacement of the timberline by about 800 m along the terrain (shorter for steeper slopes). If the predicted climate is realized in 50 years, the upward migration of *Betula pubescens* will be 16 m/year. This is quite realistic (compare Figures 12 and 13). In horizontal areas in temperate and boreal parts of the world, a 2 °C temperature rise will correspond to a climatic displacement northwards of perhaps 200-400 km, that is, a shift of 4-8 km/year (compare Cohn 1989). I think these figures are too high for most vascular plant species to cope with. Under rapid climatic change, mountainous topography which includes a large number of physical niches is no doubt favourable for the survival of a high diversity of plant and animal species. Roberts (1989) mentions this as an important physical factor for the survival of douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*) and western hemlock (*Tsuga heterophylla*) in western North America, as they can move upslope into the Rockies.

Due to migration barriers, invasion of many new species to the transect from the south in the course of 50 years is not very probable. Some weeds will be exceptions to this (see Table 1 in Ketner, this volume). However, a quantitative change in the flora and vegetation, including a shift of vegetation zones, may take place. The most rapid responses will probably be in vegetation influenced by cultural activity, which will perhaps become still more weedy. Efficient migrators with light seeds will be favoured, for example *Epilobium angustifolium*, species belonging to the family Asteraceae (*Taraxacum* spp., *Lapsana communis*, *Cirsium* spp., *Senecio* spp.), and *Salix caprea*, *Betula pubescens*, *B. pendula* and *Populus tremula*.

Nitrophilous species in the new temperate zone and in the hemiboreal zone may also be favoured, due to the more rapid decomposition rate in the soil (Falkengren-Grerup 1986).

It is predicted that the new temperate zone in the transect studied (see T in Figure 13) will be both weedy, thermophilous and nitrophilous in its new floristic composition, though carrying very few real temperate species. In addition to the above-mentioned species, those which are expected to increase, since they are thermophilous, nitrophilous and also efficient migrators, are *Arctium* spp, *Alliaria officinalis*, *Aegopodium podagraria*, *Geranium robertianium*, *Sambucus* sp, *Geum urbanum*, *Holcus lanatus*, *Holcus mollis* and *Rubus* spp. There are already signs that some of these species are rapidly increasing in Central Norway (own observations), for example *Alliaria officinalis*, *Geum urbanum*, *Holcus lanatus*, *Holcus mollis* and *Rubus* spp., so far as much a result of changed land use as of on-going climatic changes.

Within 50 years it is probable that *Ulmus glabra* will show a marked increase in the hemiboreal (HB) and southern boreal zones (LB), replacing *Betula pubescens* in low herb and some tall herb sites on south-facing slopes. The herb layer of those sites will probably show a parallel change towards becoming more thermophilous, involving invasion of *Clinopodium vulgare*, *Epipactis helleborine*, *Brachypodium sylvaticum*, *Bromus benekenii*, *Sanicula europaea*, etc.

The current low alpine zone and the lower parts of the middle alpine zone will be invaded by *Betula pubescens* and species from the upper boreal zone (UB) in places with a favourable snow cover. However, the biological processes, including migration of species, will be slower at higher levels.

The predicted milder winters (+4 °C for the winter months) will result in much higher thermic oceanicity in the transect. Figure 14 illustrates the vertical distribution of thermic oceanicity based on phytogeographical criteria, that is, on eastern (frost limits) and western distribution limits mainly determined by winter temperature (see Figures 5-9).

The zone with the currently highest thermic oceanicity, TI, is characterized by a group of plant species which are fairly sensitive to low winter temperatures. The most typical ones for the TI section are *Hypericum pulchrum* (Figure 5), *Chrysosplenium oppositifolium*, *Lonicera periclymenum* and *Ilex aquifolium*. Section TI is also defined by *Aconitum septentrionale*, *Hypericum hirsutum*, *Scirpus hudsonianus* and *Corydalis intermedia* among the eastern southwest coast avoiding plants. Other good indicators of the thermic oceanicity sectors are *Erica tetralix* and *Pedicularis sylvatica* (boundary TII/III from the west), *Blechnum spicant* and *Thelypteris limbosperma* (boundary TIII/IV from the west) and *Cornus suecica* (boundary TIV/V from the west).

The predicted climate defines a thermic oceanicity for a new section, TO (see Figure 15), in coastal Central Norway, which today is more characteristic for the British Isles (January mean temperature about 5 °C). Section TO in Central Norway will develop potential habitats for extremely frost-sensitive species like *Vicia orobus*, *Erica cinerea*, *Scilla verna*, *Endymion nutans*, *Hypericum elodes*, *Hypericum androsaemum*, *Carex laevigata* and *Wahlenbergia hederacea*. In addition, due to the predicted warmer summers (+2 °C), southern atlantic heath species, like *Genista anglica* and *Ulex europaeus*, will have their climatic demands satisfied in the new TO section in Central Norway. In the Dovrefjell area, the winters will be less severe and the more extreme southwest coast avoiding boreal and alpine plants, which today characterize section TV from the east, may be forced to retreat eastwards and upwards, or their existence may be threatened. In the transect studied, section TV will be squeezed out and replaced by TIV (see Figures 14 and 15).

Summary

A basic study of the phytogeography and autecology of 150 plant taxa in Central Norway, including mapping their vertical distribution, has been found very suitable for studying the effect of climatic change. The vertical distribution of the plant taxa has been correlated with the climate factors of summer temperature, winter temperature and yearly precipitation. This material enables **correlative modelling** of future changes in flora and vegetation. The very steep topographic and climatic gradients in the transect studied also make the material well suited for a research and monitoring programme that includes studies of ecotones, species migrations and displacement of vegetation zones and sections.

Hypotheses for explaining the cause/effect relationship between climate and vertical plant distribution are, in simplified terms:

1 **thermic oceanicity** is decisive for frost-sensitive coastal plants and complementary southwest coast avoiding continental plants,
2 **summer temperature** is decisive for thermophilous lowland plants and complementary mountain plants,

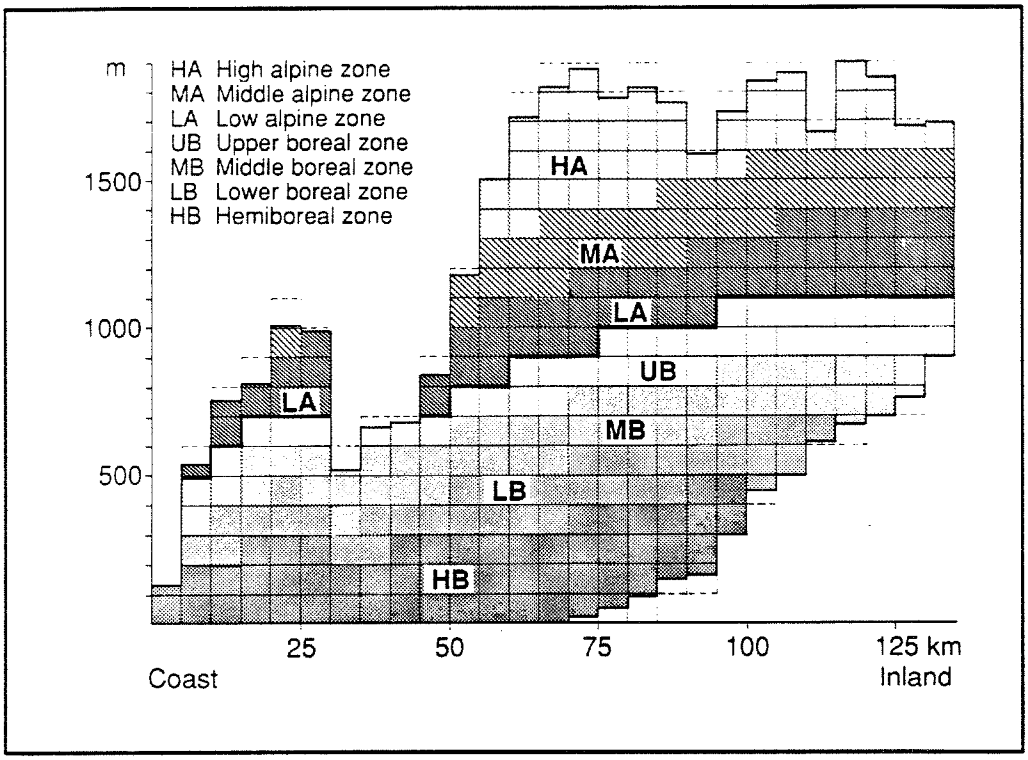


Figure 12 The current position of vertical vegetation zones for south-facing slopes in the coast-inland transect, based on phytogeographical criteria.

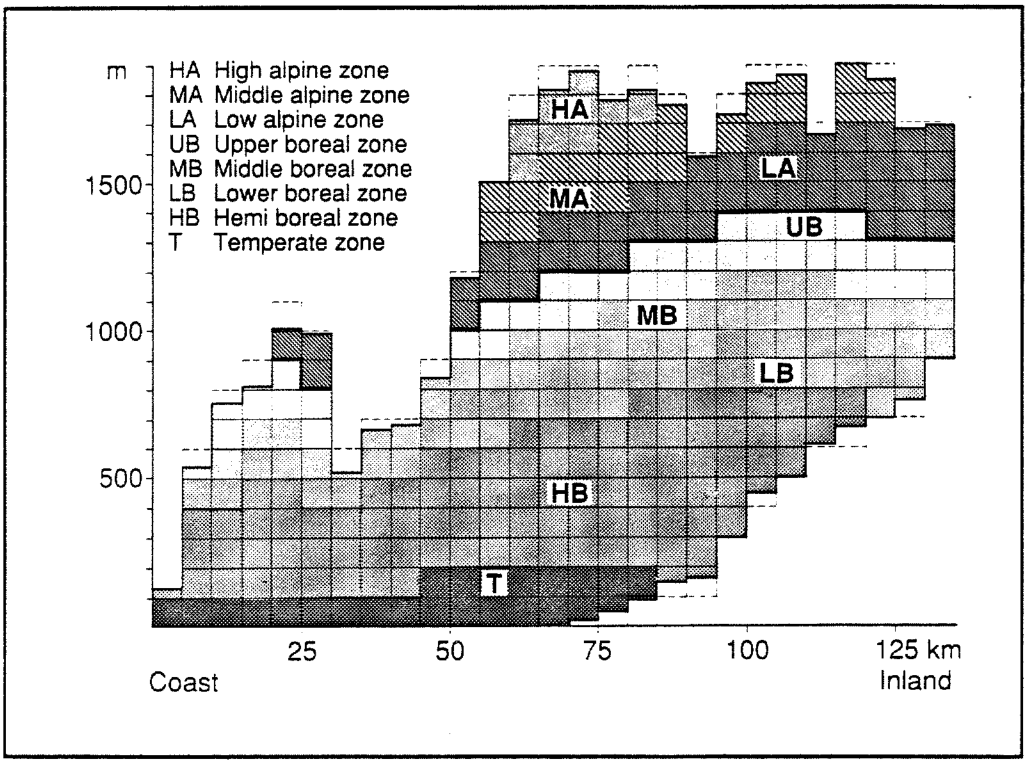


Figure 13 The predicted position of vertical vegetation zones for south-facing slopes in the coast-inland transect.

Figure 14 The current position of thermic oceanicity sections based on eastern limits of frost-sensitive species and western limits of south-west coast avoiding plants.

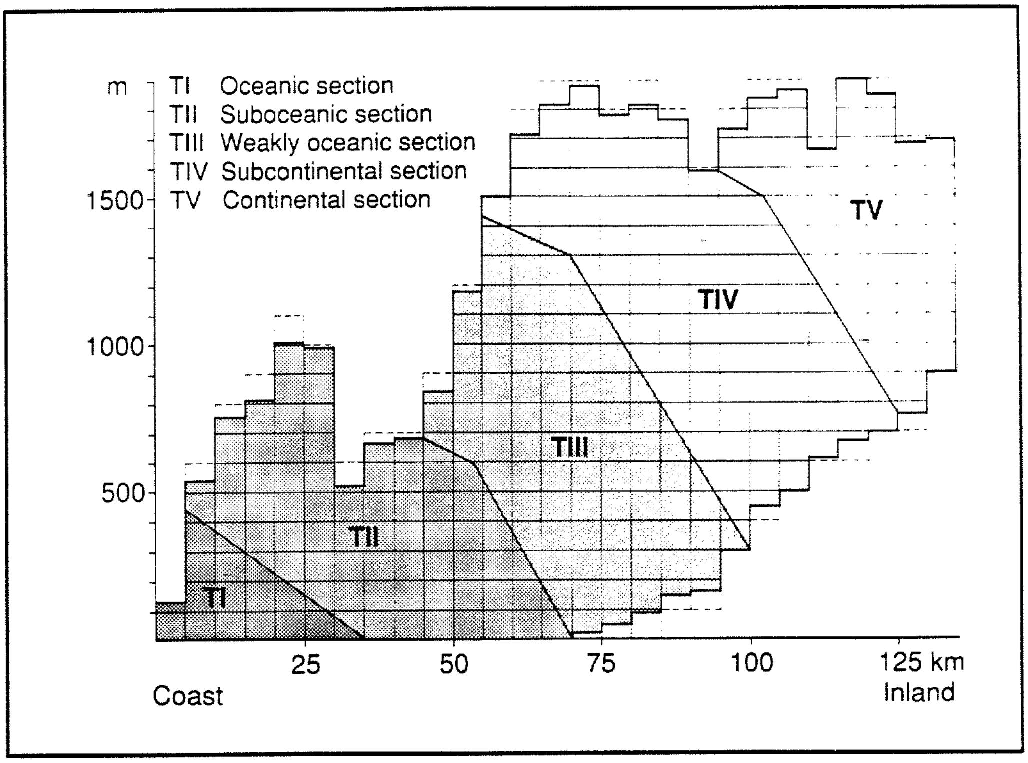
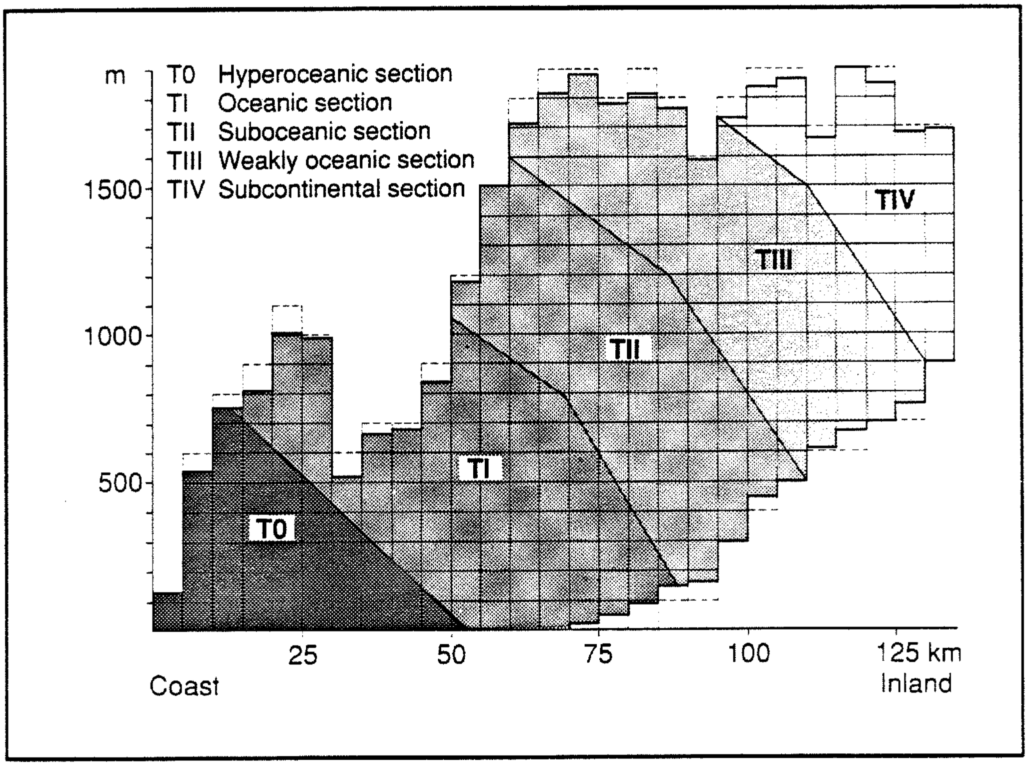


Figure 15 The predicted position of thermic oceanicity sections, including the new section TO and excluding the current section TV (compare Figure 14 and see text).



3 **humidity** is decisive for certain humidiphilous coastal species and complementary xerophilous continental species.

The following predictions of the response of species groupings are made, based on the Norwegian climate scenario (doubled atmospheric CO_2 leads to 2 °C temperature increase in the summer months and 4 °C increase in the winter months).

- **Frost sensitive coastal** plants will expand eastwards and upwards in the transect (*Hypericum pulchrum*).
- **Southwest coast avoiding continental plants** will retreat eastwards (*Viola mirabilis*); some may be threatened (*Carex heleonastes*).
- The fate of **humidiphilous coastal** plants is more uncertain. They will probably retreat at their eastern and lower limits (*Blechnum spicant*).
- **Xerophilous continental plants** may expand both upwards and westwards and replace relatively mesic sites dominated by *Vaccinium myrtillus* with *Festuca ovina* heaths.
- **Thermophilous plant species and communities** will expand both eastwards and upwards in the transect. The response of wych elm (*Ulmus glabra*) may be rapid and the tree may in a few decades invade neighbouring habitats of low and tall herbs with *Betula pubescens*.
- **Mountain plants** will retreat in both area and diversity due to the predicted elevation of the timberline. Some middle alpine species are threatened above about 1400 m (*Campanula uniflora*).

The total diversity of plants may increase somewhat in the warmer temperate and hemiboreal zones of the transect.

The main changes in flora and vegetation will be **quantitative**, at least for the next 50-100 years.

Migration barriers, mostly physical (open sea, fjords and mountains), will probably be very effective and retard the invasion of thermophilous temperate species from Central Europe and frost-sensitive species from the British Isles.

Rapid climatic change may cause strong interspecific competition in the currently established vegetation and possibly lead to local extinction of some **ecologically specialized and rare species** in the transect, for example species with high nutrition demands (*Schoenus ferrugineus*). The **generalists** (e.g. *Epilobium angustifolium*) are no doubt best adapted to rapid climatic change. At intermediate altitudes (500-1000 m), the current northern and alpine plant species will probably be replaced by the more competitive lowland species at their lower limits. (Example: *Cicerbita alpina* may in part be replaced by *Campanula latifolia*).

In central and inner fjord districts it is predicted that the vegetation zones will be elevated by about 200-300 m; in the more continental valleys by about 300-400 m. These figures are also valid for the timberline.

A new temperate lowland zone (T) will allow Central European species to grow on south-facing, lowland slopes in the transect, and **a new thermic oceanic section** (TO) will include climatic niches for very frost-sensitive species which are today confined to the British Isles and Southwest Europe. The middle and high alpine zones will be greatly reduced in the transect.

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4 Summary

Grammeltvedt

The most likely climatic changes in Norway resulting from a doubling of atmospheric CO_2 are a 3-4 °C increase in the average winter temperature and an increase of about 2 °C in the average summer temperature. Precipitation will probably increase in every season and soil moisture will increase during winter, but decrease during summer.

Dahl

The predicted climate will result in a **longer production season** and **higher agricultural production** in Norway. Some districts in Norway may become important areas for the production of fodder and root crops. **New cultivars** of agricultural plants must be developed in response to the changed climatic conditions, with the help of modern plant breeding methods.

The situation seems likely to be the opposite for forest trees. They have only **limited possibilities for genetic adaptation** in the course of 50-100 years, due to the relatively long life span of tree species. For Europe as a whole, the predicted winter temperature conditions will cause the frost-sensitive beech (*Fagus sylvatica*) to move eastwards from the present-day -3 °C isotherm for January to the -7 °C isotherm. The prospect for Norway spruce (*Picea abies*) is the opposite of beech. Its southwestern distribution limit correlates well with the present-day -2 °C isotherm for January. Under the greenhouse effect, it is expected that Norway Spruce will correlate well with the present-day -6 °C isotherm for January, with the result that spruce may disappear from lowland tracts of Northern and Central Europe. In Northern Europe, spruce and pine will probably be replaced by beech and oak (mainly *Quercus robur*).

The phenological cycle of many plant species may be disturbed by a rapid climate change, resulting in extinction of local populations.

Skre

Under the predicted greenhouse effect, distribution limits will generally move towards more arctic and alpine areas because of higher respiration in summer and a longer growing season.

The effect of a higher winter temperature will tend to be greater in a plant with an oceanic distribution.

The expected temperature increase will not only result in much **higher growth rates**, but also in **lower sink strength** and **available energy resources**, particularly in fast-growing species and ecotypes. **Photosynthesis** may take over as a growth limiting process and cause many plant species to have a narrower distribution.

Håbjørg
Natural plant species in Scandinavia vary greatly in their adaptability to changing climatic conditions. Arctic and alpine ecotypes seem to be poorly adapted to southern and maritime conditions, and southern ecotypes are poorly adapted to arctic and continental conditions. A change to above zero winter temperatures may damage highly specialized arctic and continental ecotypes.

Liljelund
In Southern Sweden, the predicted climate will probably result in **increased plant diversity**, because the immigration rate will be higher than the extinction rate. Vegetation changes will occur as a result of this **immigration/extinction process**.

Destabilization of ecosystems will probably take place, including a change from competitive species towards more ruderal species. Several ecological relationships may be disturbed: host - parasite, plant - herbivore, predator - prey, etc.

Ketner
Lags in the response of vegetation to change in climate may occur for many reasons, such as **effective geographical dispersal barriers** (physical and anthropogenic), **poor accessibility** because of unfavourable edaphic conditions, **low adaptability** to the changed length of day, **competition** from resident plants, direct and indirect effects of **atmospheric pollution** (e.g. accumulation of nitrogenous deposits in the soil), **ecotypic variation** within the range of a species and **inadequate dispersal capacity and migration rate**.

Because of a large number of **retarding factors**, changes in flora and vegetation in the coming 50 years will therefore probably not be as large as climatic change would allow. The whole process of competition in a community itself may take many decades to work through into a visibly changed natural vegetation. Extreme climatic events may enhance certain developments, for instance catastrophic death of forests caused by drought or frost.

In general, **thermophilous species** will be favoured by the predicted temperature increase. **C4 species** may have advantages over C3 species; fast-growing and fecund species will be favoured. Many species of this type are weedy species, thus contributing to **a weedification of northwest Europe**.

Holten
A basic work on the phytogeography,autecology and vertical distribution of 150 plant species along a coast-inland transect in Central Norway has been found suitable for **correlative modelling** of future floristic gradients. It can form the basis for a research and monitoring programme including studies of ecotones, species migrations and displacement of vegetation zones and sections. The effect scenario is based on the Norwegian climate scenario and hypotheses for the explanation of cause/effect relationship between climate and vertical plant distribution. The hypotheses apply the three main abiotic factors, **thermic oceanicity**, **summer temperature** and **humidity**, as limiting factors for vertical plant distribution.

The predicted responses in Central Norway of different species' groups are:
- frost-sensitive coastal plants will expand
- southwest coast avoiding plants will retreat or be threatened
- humidiphilous coastal plants will probably retreat
- xerophilous continental plants may expand
- thermophilous plants will expand
- mountain plants will retreat

In the warmer zones, the total diversity of plants may increase. During the next 50-100 years, the main change in the flora and vegetation in Central Norway will be **quantitative. Migration barriers** will effectively retard the invasion of temperate species from Central Europe.

Ecologically specialized and **rare species** in the transect may become extinct due to strong interspecific competition, and typical **generalists** will be favoured.

The vegetation zones and the timberline will be elevated by 200-300 m in the fjord districts and 300-400 m in the inner valley districts.

A new vegetation zone, the **temperate zone** (T), will develop in the lowlands, and a new **thermic oceanic section** (TO) will have climatic niches enabling an invasion of some very frost-sensitive species from

Southwest Europe and the British Isles. However, this migration process will be very slow.

5 Sammendrag

Grammeltvedt
De mest sannsynlige klimaforandringene i Norge på grunn av fordobling av CO_2-innholdet i atmosfæren, er 3-4 °C økning for vintermånedene desember, januar og februar, og en økning på 2 °C for sommermånedene juni, juli og august. Nedbøren vil sannsynligvis øke i alle årstider, jordfuktigheten vil øke om vinteren, og avta om sommeren.

Dahl
De forutsagte klimaendringene vil føre til en **lengre produksjonssesong** og **høyere jordbruksproduksjon** i Norge. Noen distrikter i Norge kan bli viktige områder for produksjon av fór og rotfrukter. Nye kultivarer av kulturplanter må bli utviklet som svar på endrete klimaforhold, ved hjelp av moderne planteforedlingsmetoder.

Situasjonen synes å være motsatt for treslagene. De har bare begrensete muligheter til genetisk tilpasning i løpet av 50-100 år, på grunn av relativt lang levetid for treslag. For Europa vil de forutsagte vintertemperaturforholdene forårsake at den frostømfintlige bøken (*Fagus sylvatica*) vil forflytte seg østover fra dagens -3 °C-isoterm for januar til -7 °C-isotermen. Utsiktene for gran (*Picea abies*) er det motsatte av bøk. Granas sørvestlige utbredelsesgrense korrelerer bra med -2 °C-isotermen for januar. Under drivhuseffekten er det forventet at granas sørvestlige utbredelsesgrense i Europa vil korrelere bra med dagens -6 °C for januar, med det resultat at grana vil forsvinne fra lavlandsområder i Nord- og Sentral-Europa. I Nord-Europa vil gran og furu trolig bli erstattet med bøk og eik (vesentlig (*Quercus robur*) på lavere og midlere høyder.

Den fenologiske syklus for mange plantearter kan bli forstyrret av raske klimaendringer, noe som kan føre til utryddelse av lokale plantepopulasjoner.

Skre
Under den forutsagte drivhuseffekten vil utbredelsesgrenser generelt forflyttes mot arktiske og alpine områder, på grunn av høyere respirasjon om sommeren og en lengre vekstsesong.

Virkningen av høyere vintertemperaturer vil ha en tendens til å være større hos planter med oseanisk utbredelse.

De forventete temperaturøkningene vil ikke bare føre til **høyere vekst-rater**, men også til **lavere "sink strength"** og **tilgjengelige energiressurser**, særlig hos raskt-voksende arter og økotyper. **Fotosyntesen** kan komme til å overta som vekst-begrensende faktor og forårsake at mange plantearter får en snevrere utbredelse.

Håbjørg
Naturlige plantearter i Skandinavia varierer mye i deres tilpasningsevne til endrete klimaforhold. Arktiske og alpine økotyper synes å være dårlig tilpasset til sørlige og oseaniske forhold, og sørlige økotyper er dårlig tilpasset til arktiske og kontinentale forhold. En forandring i vintertemperaturen til over 0 °C, kan skade de svært spesialiserte arktiske og kontinentale økotypene.

Liljelund
I Sør-Sverige, vil det forutsagte klimaet sannsynligvis føre til **økt plante-diversitet** fordi "innvandringshastigheten" (immigration rate) vil være høyere enn "dødsraten" (extinction rate). Vegetasjonsendringer vil finne sted som et resultat av denne innvandrings/døds-prosessen.

Destabilisering av økosystemer vil sannsynligvis finne sted, dette innebærer en forandring fra konkurransesterke (competitive) arter til "ugrasaktige" (ruderale) arter. Flere økologiske relasjoner kan bli forstyrret: Vert-parasitt, plante-graseter, predator - bytte, etc.

Ketner
Tidsforskyving i responsen hos vegetasjonen til forandringer i klimaet kan finne sted, slik som **effektive geografiske spredningsbarrierer** (fysiske og antropogene), **dårlig tilgjengelighet** på grunn av ugunstige jordbunnsforhold, **dårlig tilpasningsevne** til forandringer i daglengden, **konkurranse** av allerede etablerte arter, direkte og indirekte virkninger av **atmosfæreforurensing** (f.eks. akkumulering av nitrogenforbindelser i jorda), **økotypevariasjon** innen en arts utbredelsesområde og **dårlig spredningsevne og migrasjonshastighet.**

På grunn av et stort antall av forsinkende faktorer, vil forandringer i flora og vegetasjon de neste 50 årene derfor ikke bli så stor som klimaforandringene skulle tilsi. Selve konkurranseprosessen i et plantesamfunn må sannsynligvis virke flere tiår før man kan se synlige forandringer i den naturlige vegetasjonen. Ekstreme klima-episoder kan forsterke visse utviklingstendenser, f.eks. katastrofe-død av skog forårsaket av tørke eller frost.

Generelt vil **varmekjære arter** bli begunstiget av den forutsagte temperaturøkning. C4-arter kan ha fordeler framfor C3-arter; raskt-voksende og fruktbare arter vil bli begunstiget. Mange av disse artene er ugras-arter, som på denne måten bidrar til en **ugras-økning i Nordvest-Europa.**

Holten
Et grunnleggende arbeid om plantegeografien, autøkologien og vertikalutbredelsen til 150 plantearter langs et kyst-innland-profil i Midt-Norge, er funnet egnet for **korrelativ modellering** av framtidige flora- og vegetasjonsgradienter. Arbeidet kan utgjøre grunnlaget for et forsknings- og overvåkingsprogram som inkluderer studier av økotoner, artsvandringer og forflytting av vegetasjonssoner og -seksjoner. Virkningsscenariet er basert på det norske klimascenariet og hypoteser for forklaring av årsak/virkning-forholdet mellom klimafaktorer og vertikalutbredelse av plantearter. Hypotesene baserer seg på tre faktorer blant de abiotiske klimafaktorene: **Termisk oseanitet** (vintertemperatur), **sommertemperatur** og **humiditet**, som begrensede faktorer for vertikalutbredelse av planter.

De forutsagte responsene i Midt-Norge på de forskjellige økologiske plantegrupper er:

- **frost-ømfintlige kystplanter** vil ekspandere
- **sørvestkyst-skyende plantearter** vil gå tilbake eller bli truet
- **fuktighetselskende kystplanter** vil trolig gå tilbake
- **xerofile kontinentale planter** kan ekspandere
- **varmekjære arter** vil ekspandere
- **fjellplanter** vil gå tilbake, en del arter vil trues

I de varmeste vegetasjonssonene kan den totale plantediversiteten øke. I løpet av de neste 50-100 årene, vil likevel hovedforandringen i floraen og vegetasjonen i Midt-Norge være kvantitativ. **Spredningsbarrierer** vil effektivt forsinke innvandringen av varmekjære arter fra Sentral-Europa.

Økologiske spesialister og **sjeldne arter** i vertikalprofilet, kan bli utryddet på grunn av sterk interspesifikk konkurranse. Typiske **generalister** vil bli begunstiget.

Vegetasjonssonene og skoggrensa vil bli hevet ca 200-300 m i fjordstrøkene, og 300-400 i indre dalstrøk.

En ny vegetasjonssone, **den tempererte sonen (T)**, vil dannes i lavlandet, og en ny termisk **oseanitetsseksjon (TO)** vil ha klimanisjer som legger til rette for invasjon av mer frost-ømfintlige arter, som i dag bare finnes i Sørvest-Europa og på de britiske øyer, men denne migrasjons-prosessen vil være svært treg.

6 Appendix

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