

BOREAL FOREST FUTURES: MODELLING THE CONTROLS ON TREE SPECIES RANGE LIMITS AND TRANSIENT RESPONSES TO CLIMATE CHANGE.

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Abstract. Range limits and broad-scale geographic variations in the productivity of boreal and northern deciduous tree species in Europe are simulated with a bioclimatic model (STASH). STASH is based on a small number of distinct mechanisms by which climate is thought to affect the survival, regeneration and growth of trees. Survival is limited by summer warmth requirements and winter cold tolerance; regeneration, additionally by winter chilling requirements; and growth rate by net assimilation, which in turn is related to photosynthetically active radiation, growing-season length, temperature (relative to species-specific optima) and soil moisture supply (relative to evaporative demand). These mechanisms are quantified either as thresholds (for survival and regeneration) or multipliers (for growth), based on bioclimatic variables computed from monthly climate normals interpolated three-dimensionally to a 10-minute grid. Growing-season and growing degree day calculations take into account the effects of chilling. The drought calculations also take into account the effects of soil-moisture storage by means of a physically based evapotranspiration calculation coupled to a one-layer soil hydrology model. STASH is used to examine changes in potential range limits under a $2\times\text{CO}_2$ climate-change scenario. Associated transient responses at selected sites in the boreal and boreo-nemoral zones of Sweden are also simulated, using the forest gap model FORSKA2. The species-specific survival and regeneration constraints and growth responses of STASH modify the growth, establishment and mortality of trees in FORSKA2. The results obtained in this way differ sharply from the results of conventional forest gap models, where growth rates are assumed to decline to zero at minimum and maximum growing degree day limits. For example, towards the southern limit of *Picea abies* (Norway spruce), STASH correctly shows no decline in productivity, but rather an abrupt cut-off corresponding to a chilling requirement during regeneration that is not met further south or west. In transient warming scenarios, this mechanism has the effect that natural regeneration can be blocked due to the warm winters even as yield is increasing due to the longer and warmer summers. STASH predicts drastic changes in species distributions in response to the large climate changes (especially winter warming) expected for northern Europe. Some of the common boreal species (e.g., *Picea abies*; *Pinus sylvestris*; *Alnus incana*) are unlikely to survive in much of their present range, withdrawing to the far north. Other species already widespread may be able to occupy some of the few sites that are today unavailable to them (e.g., *Betula* spp.; *Corylus avellana*). Other temperate deciduous species such as *Fagus sylvatica* could have dramatic range expansions, potentially occupying large tracts of the present boreal zone. FORSKA2 transient simulations illustrate some of the possible routes towards different types of forest in a changed climate. Some sites in the north show little change in species composition, but sites towards the southern boundary of the boreal zone could develop a new suite of dominants. The degree of sensitivity of a particular site depends both on the climate change prediction and on the transient dynamics of the forest community. Many types of transient behaviour are shown to be possible. Coupled with uncertainties about the future role of dispersal and changes in disturbance rate, the complexity and variety of these transient responses imply a highly uncertain future for the north European boreal forests.

Keywords. BIOCLIMATOLOGY, CHILLING REQUIREMENTS, CLIMATE CHANGE, FOREST DYNAMICS, FOREST MODEL, RANGE LIMIT, TRANSIENT EFFECTS.

1. Introduction

Boreal forests cover large areas of land in the northern high latitudes. They could respond in dramatic ways to future climate change. The greatest degree of climate change, in the form of large and rapid increases in winter temperatures, is predicted for just these areas. Modelling approaches make it possible to assess the range of potential responses by the affected ecosystems.

Two models are used in this paper to assess possible responses of forest tree species to the climate change induced by a doubling of CO₂. The first, STASH (Sykes *et al.*, in press), uses a small number of bioclimatic limits each representing a particular, known type of constraint (growing-season heat requirement, winter cold tolerance, drought tolerance, chilling requirement) to characterise the distributions of northern European tree species under the current climate (Sykes *et al.*, in press). The success of STASH in representing the current distributions accurately with a small number of parameters is a consequence of its mechanistic basis, which also makes it meaningful to use the model to simulate future distributions under a different climate. Such simulations provide insights on the possible responses of boreal tree species' *potential* distributions to future climate change.

Further analysis of the forest dynamics, transient responses of species and overall biomass changes in affected regions can be assessed by transient modelling dynamics on a local landscape scale. This is done here using a version of the FORSKA2 model (Prentice *et al.*, 1993). FORSKA2 is a non-conventional (i.e., not derived from JABOWA) forest gap model. Bioclimatic limits for survival and regeneration, and the multipliers for growth as described in Prentice *et al.* (1993), are modified so as to be consistent with those used in STASH.

Model projections are naturally beset with uncertainties. Many hypotheses and assumptions are embodied in the models, which in any case can only give a partial picture of what may happen. For example, we have not tried to include "higher-order" effects such as possible increases in pest outbreaks due to climatic warming, nor have we considered likely management responses in any detail; and we have not included any representation of the possible modifying effects of CO₂ as a physiological (as opposed to climatic) agent. Nevertheless, our results indicate some key areas of concern and point to specific research needs (notably for more experimental information on the chilling requirements of a wide range of species) that are fundamental, even for the generalised and approximate scenarios that we are trying to develop.

2. Methods

2.1. CLIMATE DATA

The climate data set is based on weather station records of long-term mean monthly values for temperature, rainfall and sunshine (as proportion of possible sunshine hours, which is approximately the complement of average cloud cover). The data set is an updated version (W. Cramer, pers. comm., 1994) of the original dataset of Leemans and Cramer (1991). This update uses a surface fitting technique to interpolate to a 10' grid (Hutchinson, 1989). The entire window (25°E to 50°E, 35° to 75°N) was used for the STASH calculations. FORSKA2 runs were based on interpolated climate data for a few selected grid cells.

The 2×CO₂ scenario was created by using four general circulation models (GCMs) (GFDL (Manabe and Wetherald, 1987); OSU (Schlesinger and Zhao, 1989); UKMO (Mitchell, 1983), GISS (Hansen *et al.*, 1988)). Temperature and precipitation anomalies (differences between simulated 2×CO₂ and control climates) were interpolated to each 10' grid cell. These interpolated anomalies were then added to the

current climate. The mean of the four scenarios was calculated to give “mean GCM” $2\times\text{CO}_2$ datasets of monthly mean temperature and precipitation. Sunshine anomalies were not available, so the current sunshine dataset was used. A constant 150 mm soil water holding capacity was assumed.

2.2. MODELLING TREE SPECIES RANGE LIMITS

There is still surprisingly little experimental information on the controls of the natural ranges even of the most economically important of the northern tree species. However, general observations of plant physiology and biogeography serve to identify the primary controlling variables (e.g., see Woodward, 1987). *Minimum temperatures* in winter are critical for most woody species (Sakai and Weiser, 1973), and extreme low temperatures are known to cause damage or death. The key variable is the extreme temperature, but mean coldest-month temperatures are well correlated with absolute recorded minimum temperatures (Prentice *et al.*, 1992). Some level of integrated *summer warmth* (usually expressed as growing degree days) is required by all species. *Drought* is a third major limiting factor. Drought is not directly related to precipitation, but rather to soil moisture supply—or more precisely, to the extent to which soil moisture supply satisfies evaporative demand. Thus, effective drought can be indexed by the ratio of actual to potential evapotranspiration, which in turn can be estimated using soil moisture accounting models (Prentice *et al.*, 1992, 1993). STASH therefore estimates mean coldest-month temperature, growing degree days above a 5 °C base (GDD) and the drought index α (strictly, the ratio of actual evapotranspiration to the equilibrium evapotranspiration computed from temperature and net radiation, which in turn is computed from temperature, insolation at the top of the atmosphere, and sunshine) and assumes that these three factors constitute separate and independent constraints on species’ potential ranges.

In addition, northern woody species require a *period of chilling* to induce budburst in the spring. Just as specific cold tolerance and winter dormancy mechanisms confer protection against the lowest temperatures encountered during dormancy, so delayed budburst is an insurance against the possibility of low temperature damage occurring after dormancy is broken. This applied to evergreen conifers as well as to deciduous trees. The possibility of future warming in northern regions has stimulated experimental work on the subject of chilling requirements. It has been found that the chilling response is species-specific (Cannell and Smith, 1986; Murray *et al.*, 1989) and that the thermal time (i.e., the number of GDD) to budburst decreases exponentially with the chilling period. Some species (e.g. *Fagus sylvatica*) are especially sensitive to late spring frosts, and accordingly have a very high chilling requirement that implies very late budburst in regions with mild winters. Such species are however not well adapted to the most oceanic climates. STASH incorporates this trade-off by calculating an “effective” GDD (GDD°). GDD° is defined as the minimum number of required GDD, reduced by the number of GDD to reach budburst. This in turn is a function of the chilling period length. The form of the chilling response function (relation between GDD° and chilling period) was taken from Murray *et al.* (1989). For species tested by Murray *et al.* (1989), the parameters of this function were also constrained by the experimental data; Sykes *et al.* (in press) showed that including the known chilling response in this way substantially improved the range-limit

predictions in western and northwestern Europe. For other species, chilling parameters were inferred from the range limits together with the other bioclimatic limits.

STASH further imposes a maximum value of the mean coldest-month temperature on a few continental species such as *Picea abies*, to reflect their notoriously poor regeneration in oceanic climates.

2.3. MODELLING TRANSIENT RESPONSES AND FOREST DYNAMICS

Forest dynamics were simulated at sites through the boreal and boreo-nemoral zone of Sweden. [The boreal (coniferous) forest zone extends southwards to *ca.* 60°N. The nemoral (temperate deciduous) forest zone is confined to the far south and the southwest coast; the boreo-nemoral (mixed) forest zone lies in between (Sjörs, 1965; Hutisch, 1960).] The simulations were done using the forest gap model FORSKA2 (Prentice *et al.*, 1993). FORSKA2 has at its core the FORSKA model of Prentice and Leemans (1990). FORSKA2 has been developed as a general forest landscape model for use in climatic change experiments. It has been used to simulate boreal and boreo-nemoral forest dynamics and transient effects under a number of climate scenarios (Prentice *et al.*, 1991; Price *et al.*, 1993; Sykes and Prentice, unpubl. ms.; Sykes, 1994) as well as providing estimates of carbon storage in boreal forested regions under present and future climates (Price *et al.*, 1993; Sykes and Prentice, 1995).

Five sites were selected for the simulations (Figure 3), from Reivo in the north of Sweden to Boa Berg in the south, on the southwestern boundary of the boreo-nemoral zone. At each of the five sites FORSKA2 simulated 1000 yr of forest dynamics using 200 independent 0.1 ha patches, scattered over a simulated landscape. Each patch had a 100 yr root-mean-square return time for disturbance, using a formulation that gives an increasing probability of disturbance for the patch as it ages (Prentice *et al.*, 1993). Nineteen of the most common northern European tree species were "available" for establishment and growth. At one site, Tyresta in the Stockholm region, an additional simulation was done in which immigration of "new" species was disallowed.

Monthly temperature, precipitation and sunshine values for the 10' cell containing the selected site were used. In the first 400 yr of the simulation the model was allowed to come to an equilibrium under the present climate. The climate was then changed linearly over 100 years so that it reached the "mean GCM" temperature and precipitation by year 500. Once the new climate was achieved, monthly temperature and precipitation were held at the new level for a further 500 yr.

3. Results

3.1. SPECIES DISTRIBUTION LIMIT CHANGES: COMMON TREES OF THE BOREAL AND BOREONEMORAL ZONE

Picea abies (Norway spruce) is one of the major boreal forest trees in northern Europe. Its distribution is simulated well by STASH (Sykes *et al.*, in press). In particular, its complex northwestern and western boundary is described accurately: STASH shows where *Picea* is excluded from the coast in western and northern Norway and in the far south of Sweden (Figure 1). The simulation also suggests that *Picea* responds to increased temperatures towards the south, being at its most productive near its southern boundary.

Under the “mean GCM” climate scenario, where winters become substantially warmer, *Picea* establishment is predicted to fail in much of western Europe. Over time this would force a retreat eastwards, leaving only a few outposts in mountain regions (Figure 1). *Picea* would be removed from Fennoscandia except for parts of northern Sweden and Finland.

Pinus sylvestris (Scots pine), another major component of the present-day boreal forest, has a similar simulated present and future distribution to *Picea abies* (Figure 1). However the mechanisms (and past histories) behind these shifts are evidently different (Huntley and Prentice, 1993). *Pinus sylvestris* can regenerate at present in many places on the oceanic fringe of Europe where it is no longer found as a native species. Deciduous species may be outcompeting *Pinus* in the natural vegetation of these areas (Prentice *et al.*, 1991). Under a changed climate of the magnitude used here, *Pinus* declines in the boreal zone, as does *Picea*; but the implied mechanism involves competition instead of regeneration failure.

Acer platanoides (Norway maple) reaches its present northern boundary in the southern boreal zone of Sweden and Finland (Figure 1). Under the changed climate its western limit shifts, so that it is excluded from most of western Europe. *Acer platanoides* is shown at its most productive in central Europe and could still be found throughout Finland (except for the coastal strip) and in other northern or mountain regions of Norway and Sweden.

Alnus incana (grey alder) is found throughout the boreal zone today, and reaches its southern limit in the boreal-nemoral zone of southern Sweden (Figure 1). Under the changed climate it retreats both northwards and eastwards to become restricted almost entirely to northern Fennoscandia and Russia. *Betula pendula* (silver birch) occurs throughout the boreal zone except in the upper montane and northernmost regions of Fennoscandia. Under the changed climate the range of *B. pendula* increase to cover all the present boreal zone. *B. pendula* is also likely to become more productive, particularly in southern boreal regions (Figure 1).

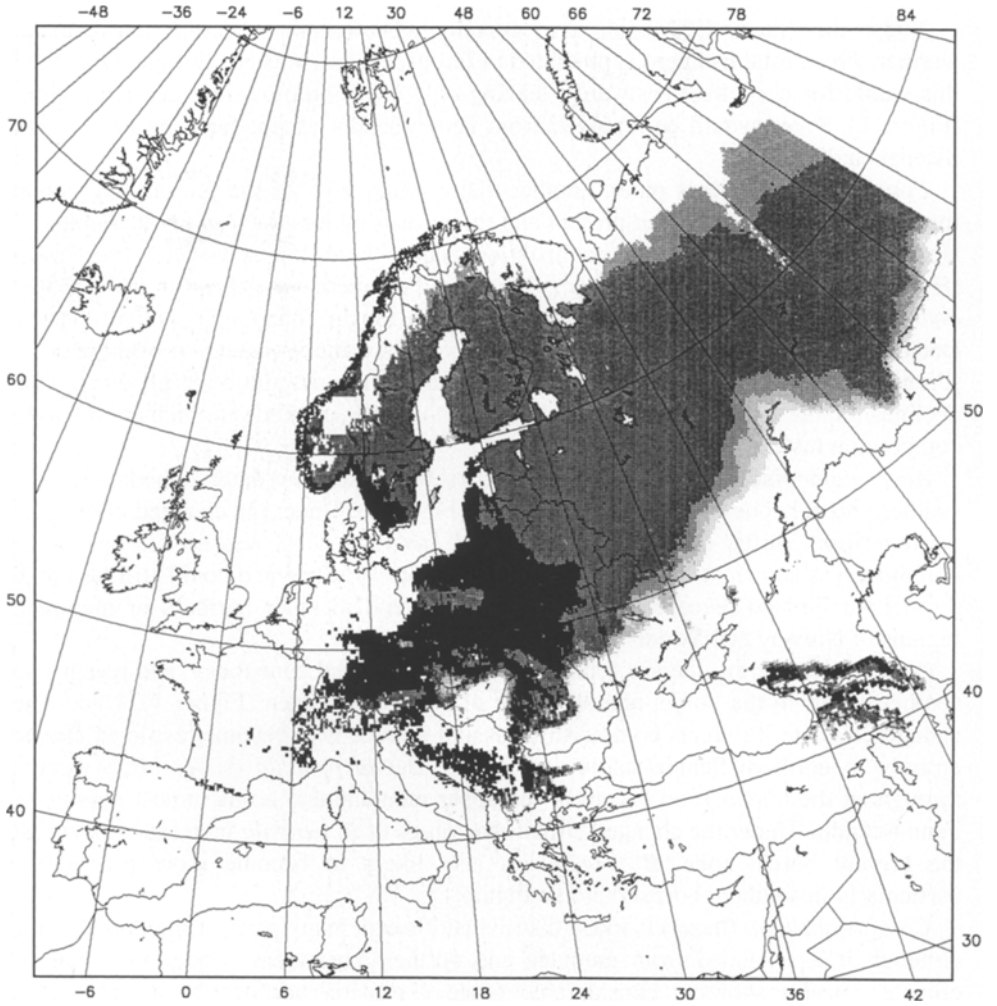
Corylus avellana (hazel) is today distributed through many parts of the boreal zone, although it is excluded from montane and northernmost areas. Under the changed climate *Corylus* shows a considerable range expansion northwards, upwards, and eastwards into Russia. In Fennoscandia only the highest elevations remain outside its range (Figure 1).

Fraxinus excelsior (ash) reaches its northern limit in central Sweden and Finland in the southern boreal zone (Figure 1). Under the changed climate it is shown extending much further north, though still excluded from the far north. It is also likely to be excluded from coastal areas in the present day southern boreal zone, where it is found at present.

Populus tremula (aspen) is common throughout the boreal and boreo-nemoral zone though excluded from the far north. Under the changed climate *Populus tremula* moves to occupy these areas too, but at the same time its range is restricted in southern coastal areas (Figure 1).

Quercus robur (pedunculate oak) has its northern limit today at the border of the southern boreal and boreo-nemoral zones (Figure 1). Under the changed climate there is a strong range expansion northwards into most of the present boreal zone.

Tilia cordata (small-leaved lime) reaches its northernmost limit in the southern boreal zone (Figure 1). Under the changed climate it expands northwards, but retreats from southern and coastal regions.



Picea abies

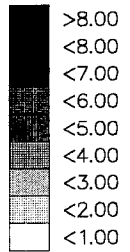
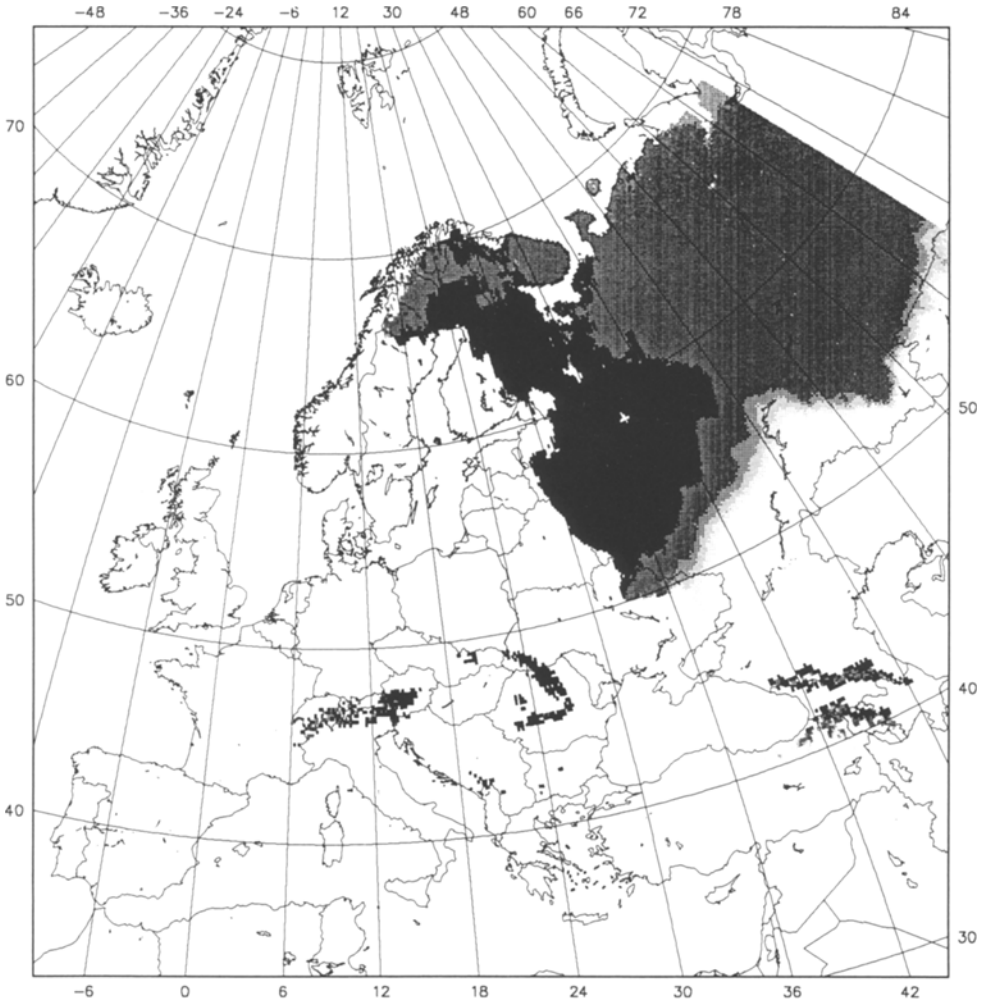


Fig. 1. Simulated distributions of 11 of the most common boreal or boreo-nemoral zone trees of northern Europe: under present climate, and under a changed climate derived from the mean of four $2\times\text{CO}_2$ scenarios.



Picea abies future climate

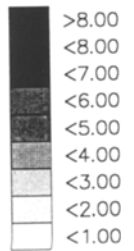
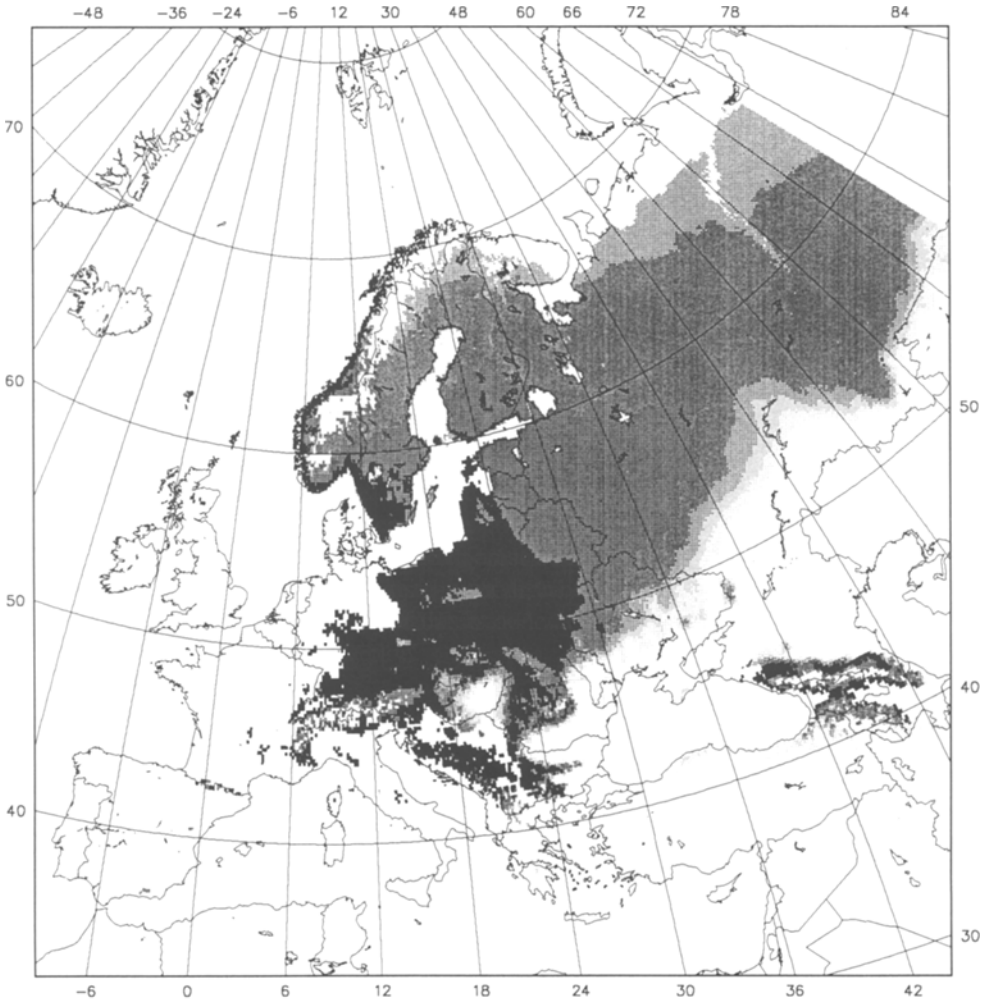


Fig. 1. (continued)



Pinus sylvestris

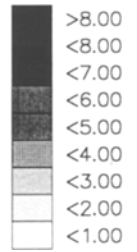
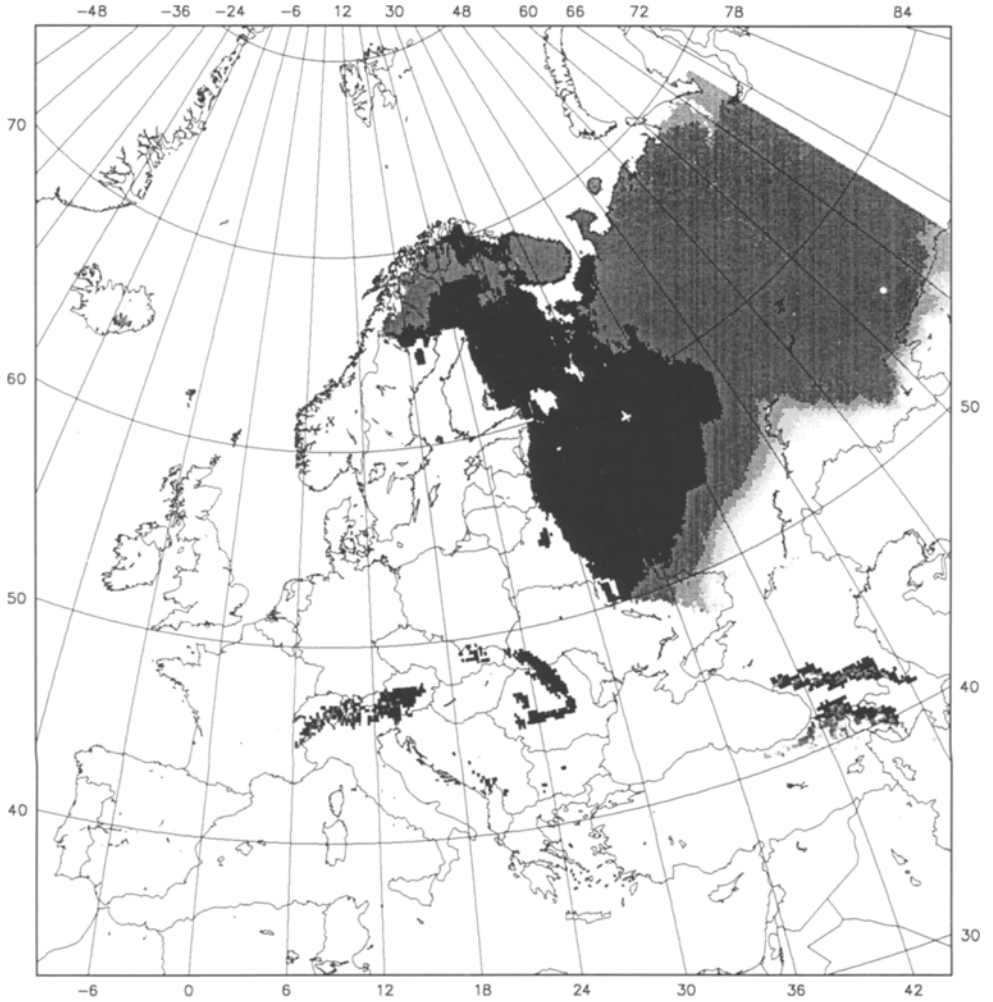


Fig. 1. (continued)



Pinus sylvestris future climate

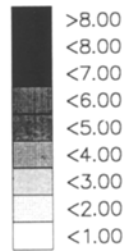
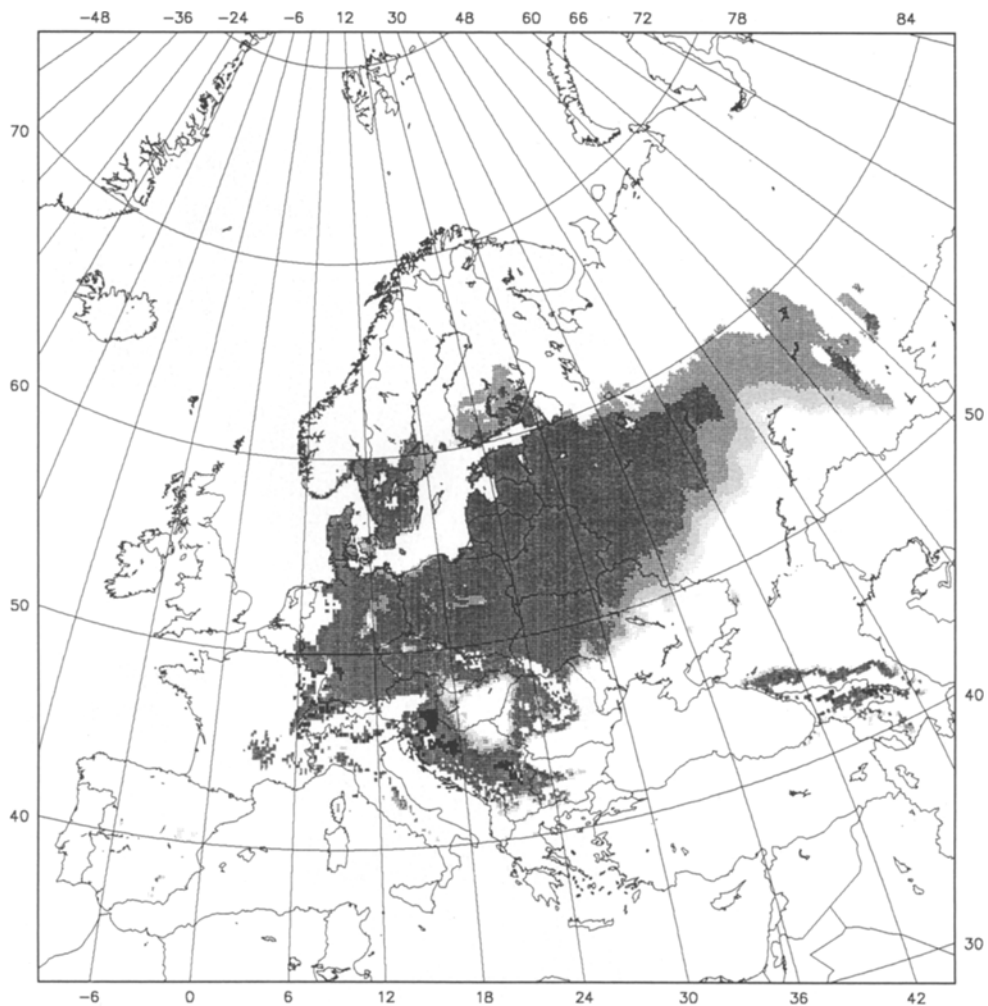


Fig.1. (continued)



Acer platanoides

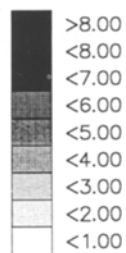
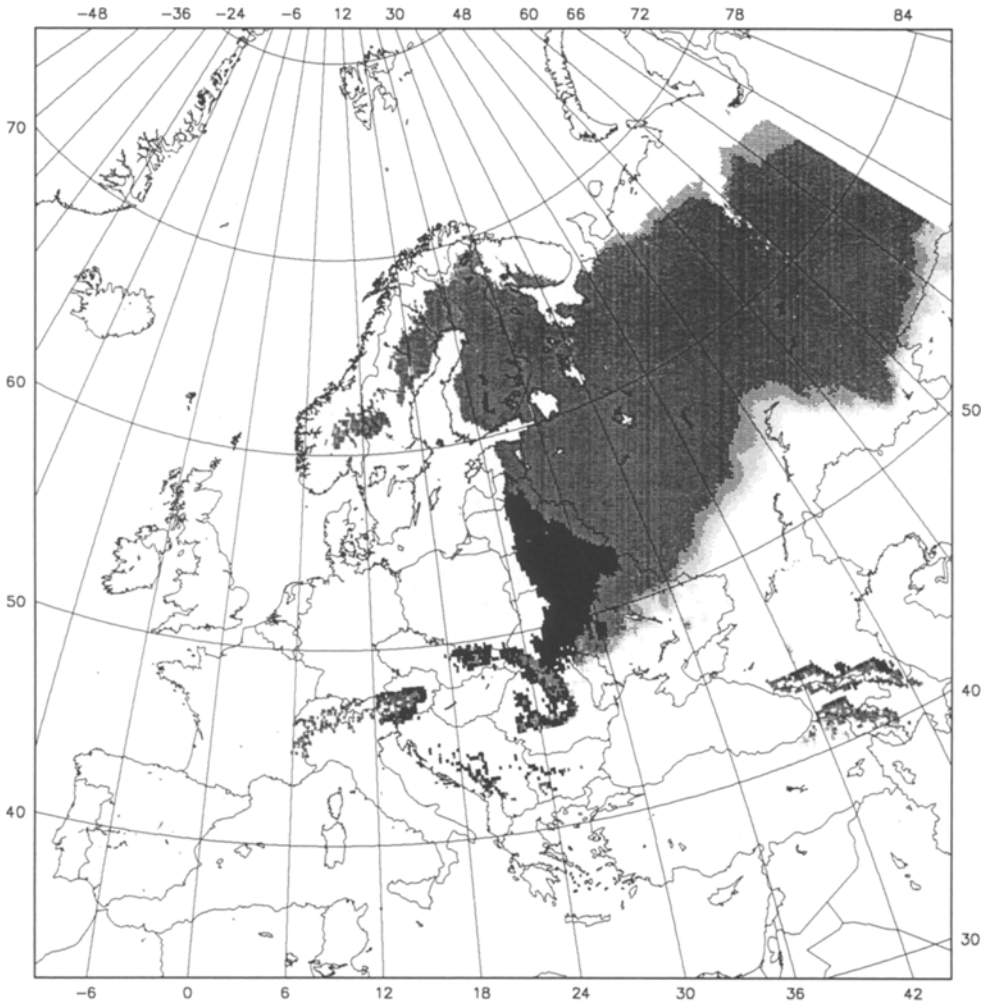


Fig. 1. (continued)



Acer platanoides future climate

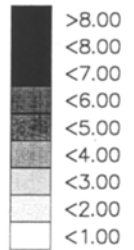
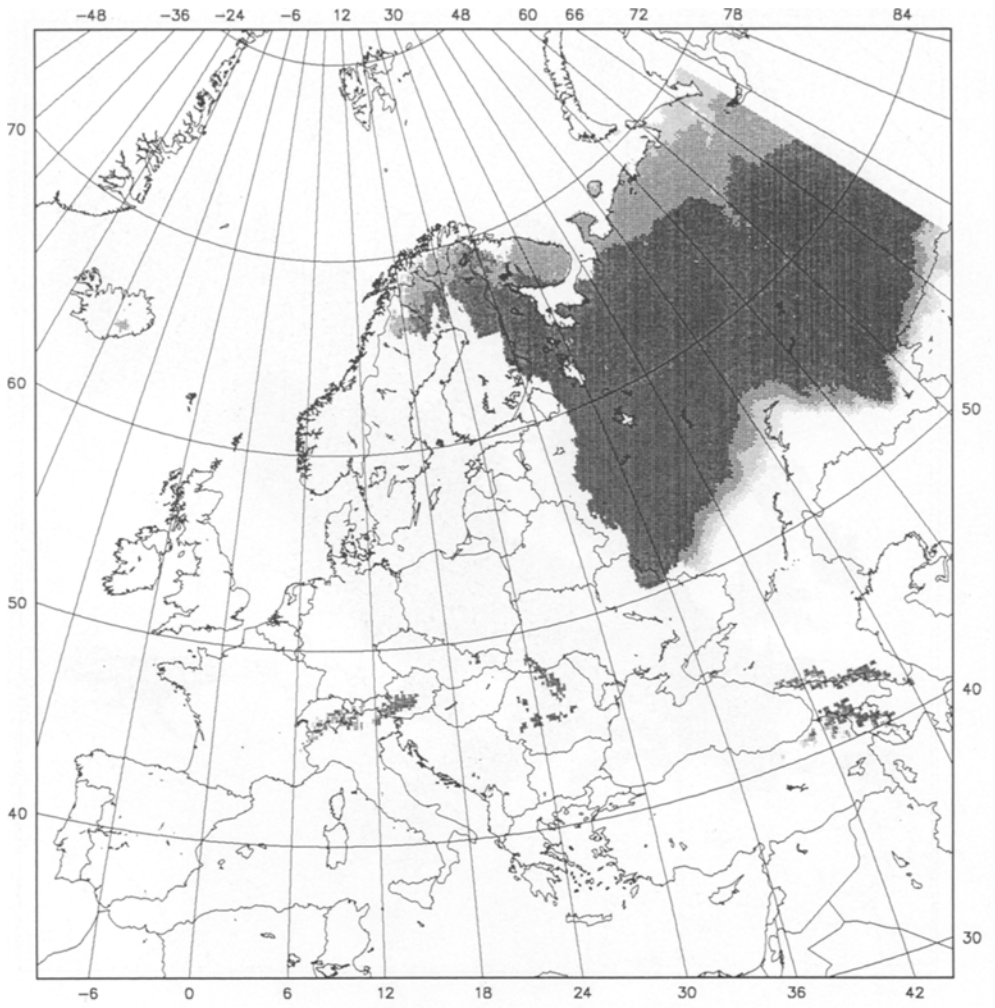


Fig.1. (continued)



Alnus incana

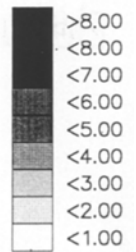
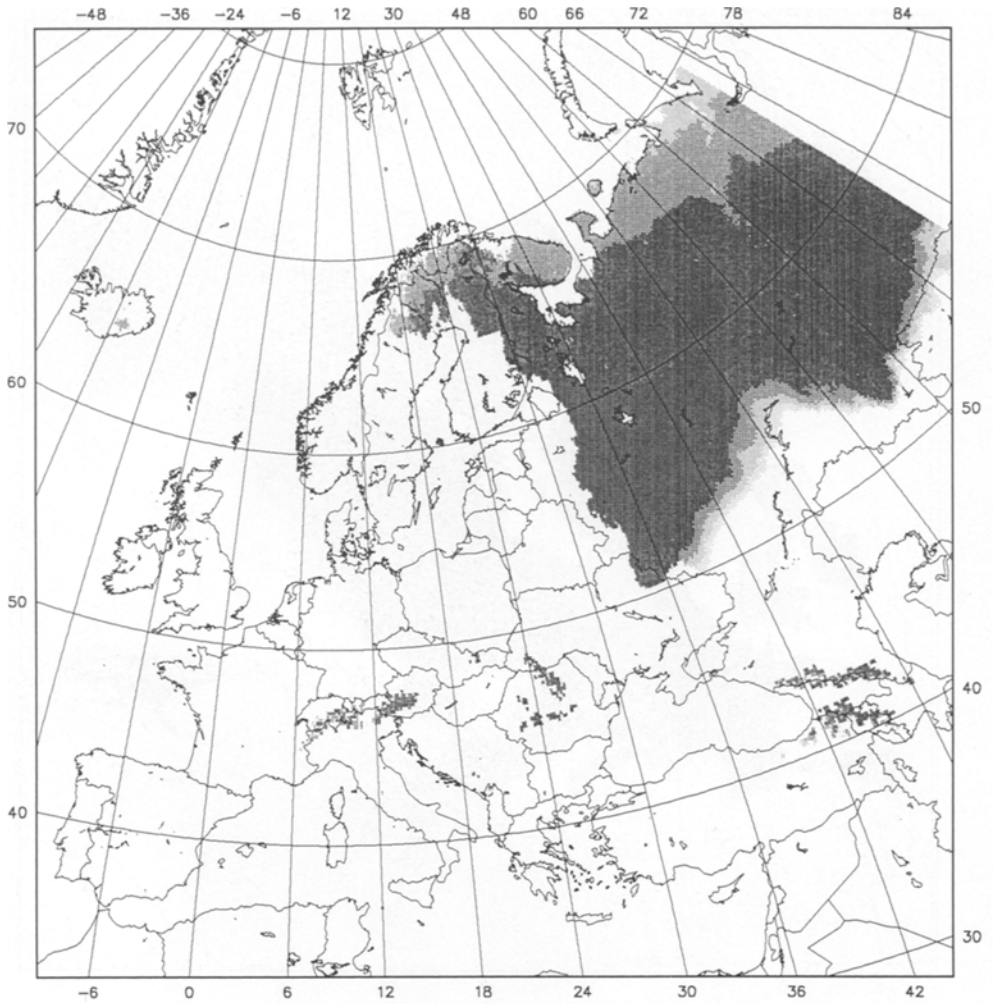


Fig. 1. (continued)



Alnus incana future climate

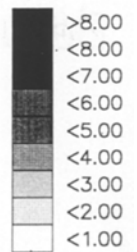
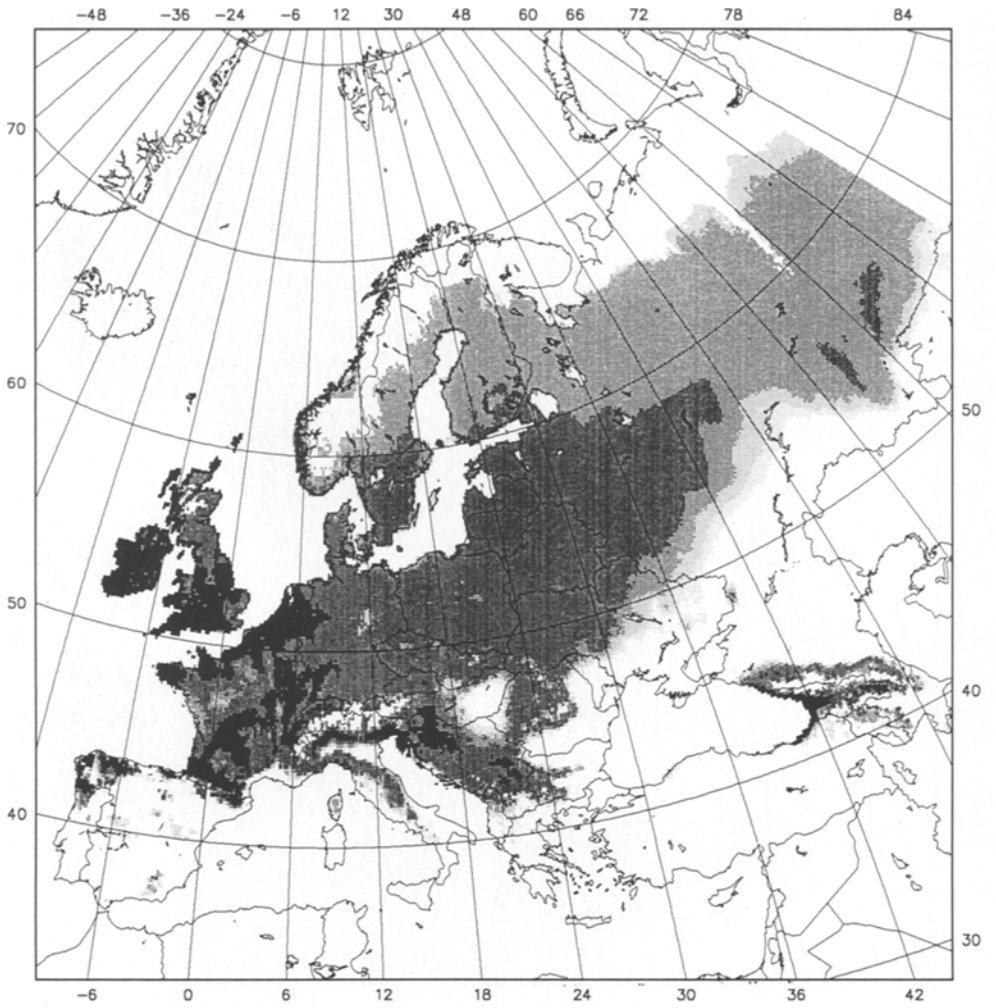


Fig. 1. (continued)



Betula pendula

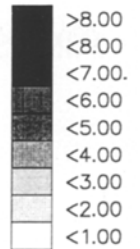
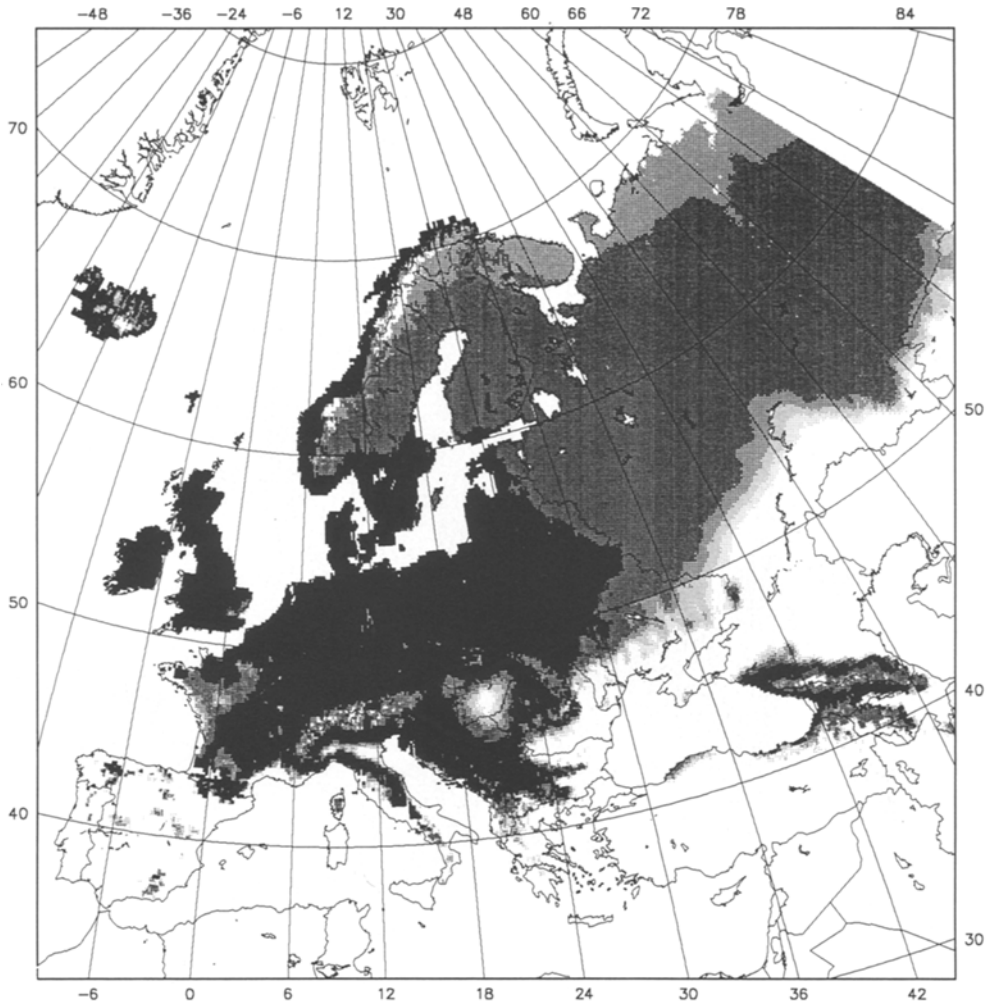


Fig.1. (continued)



Betula pendula future climate

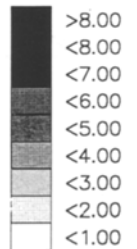
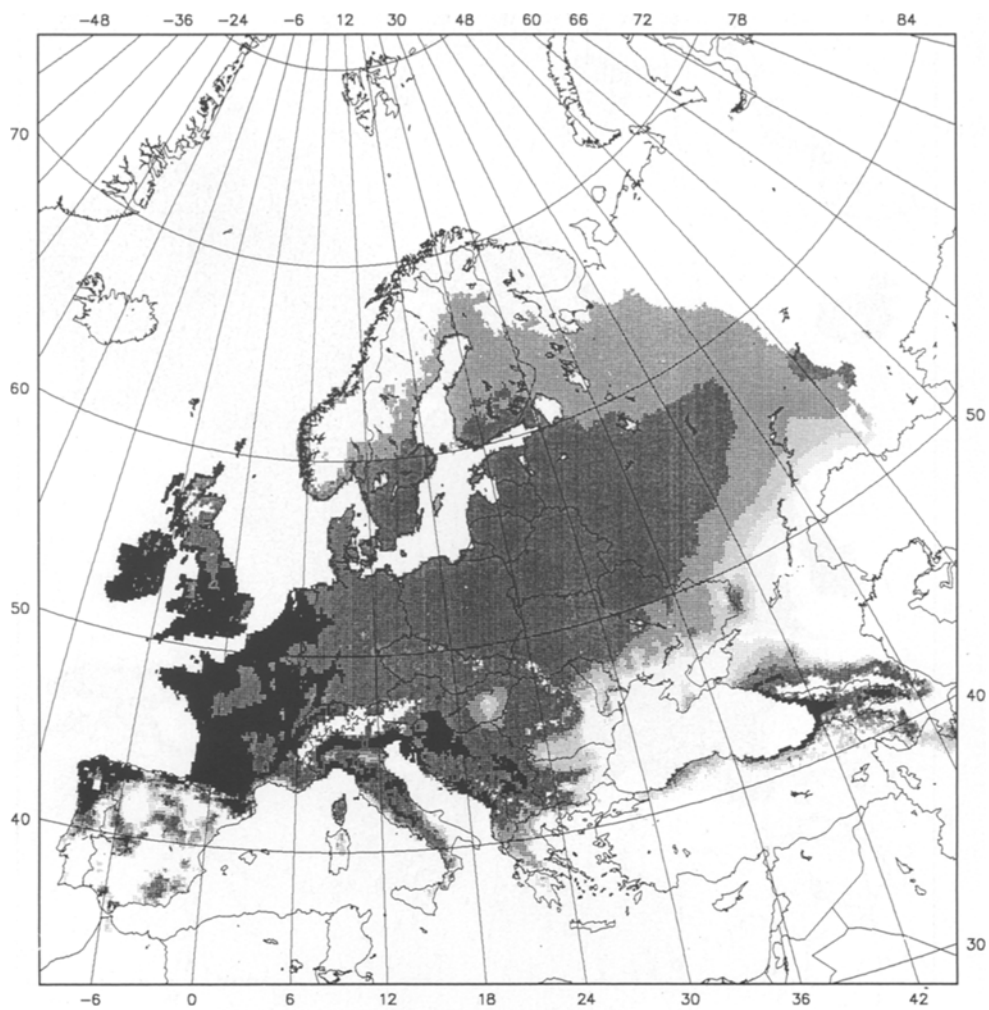


Fig.1. (continued)



Corylus avellana

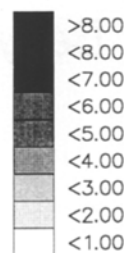
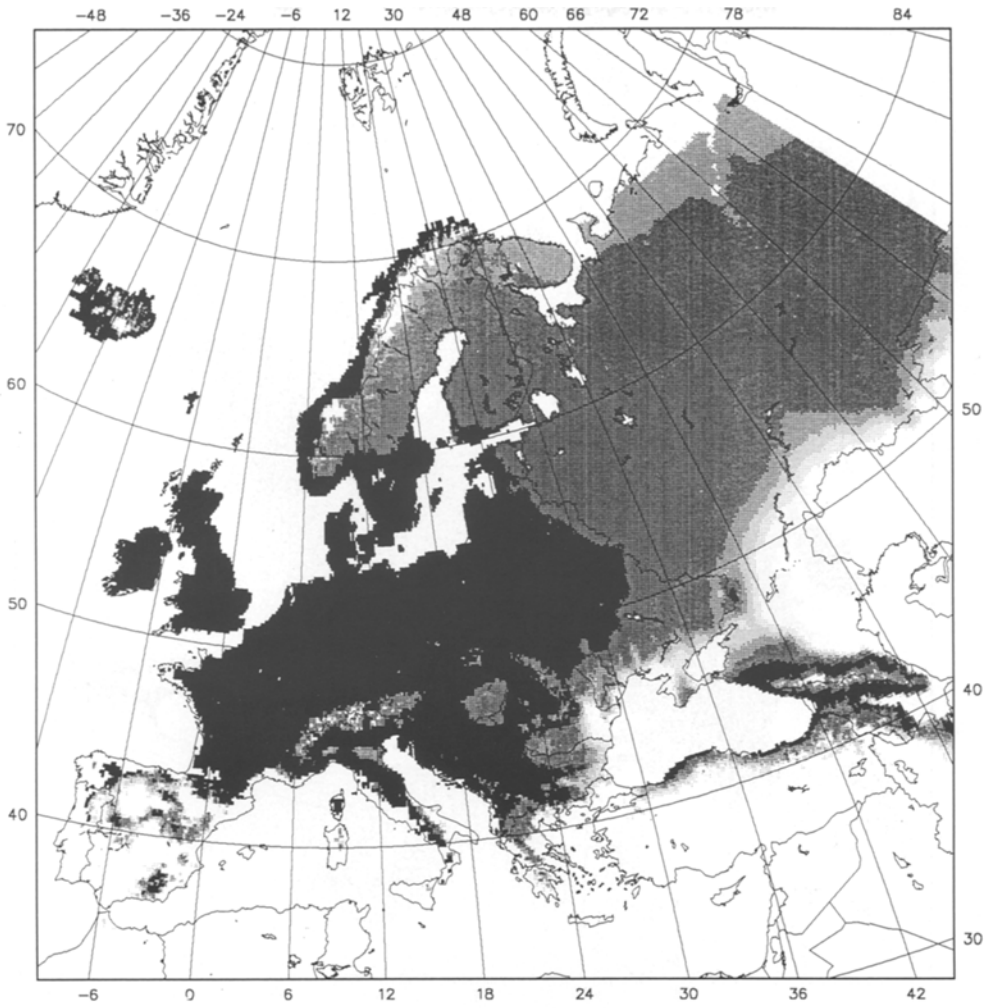


Fig. 1. (continued)



Corylus avellana future climate

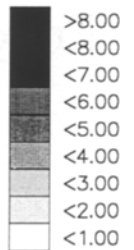
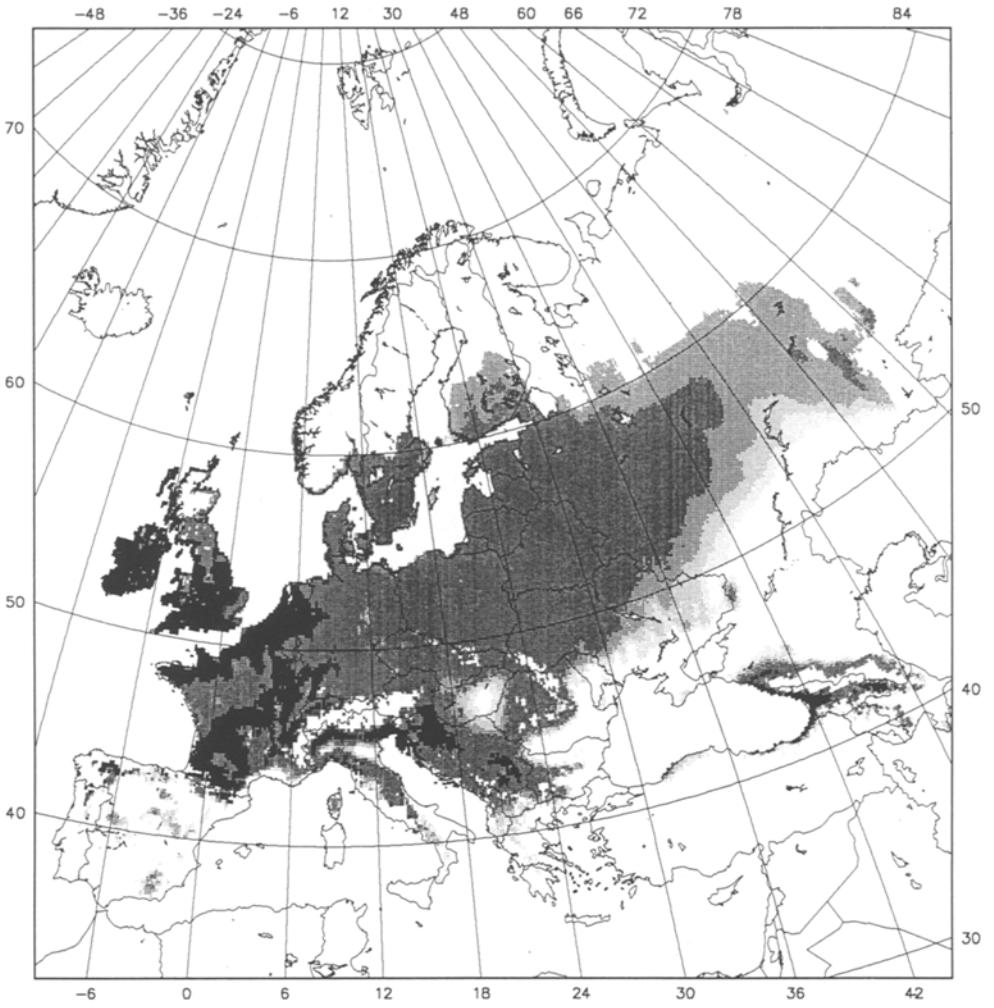


Fig.1. (continued)



Fraxinus excelsior

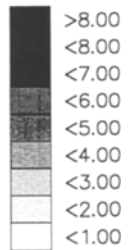
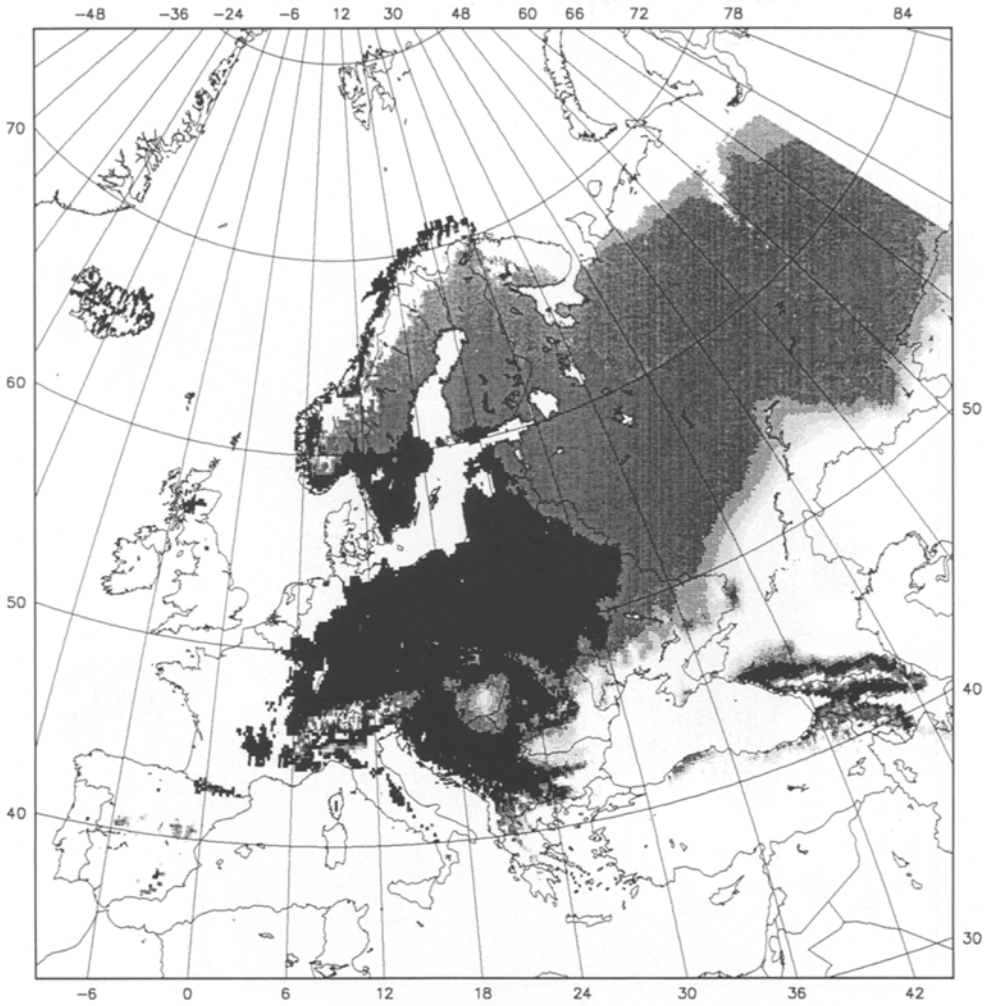


Fig. 1. (continued)



Fraxinus excelsior future climate

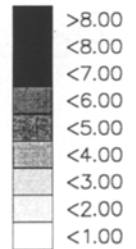
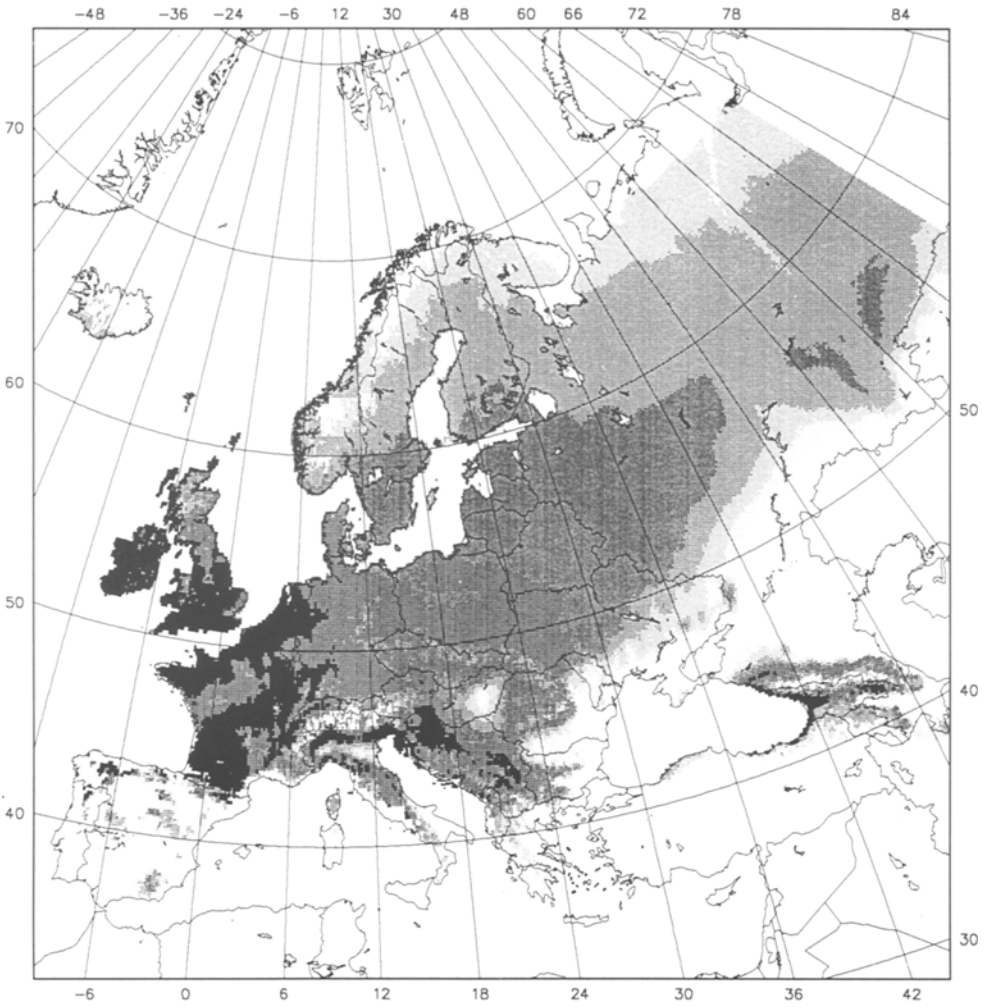


Fig. 1. (continued)



Populus tremula

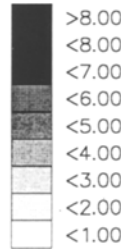
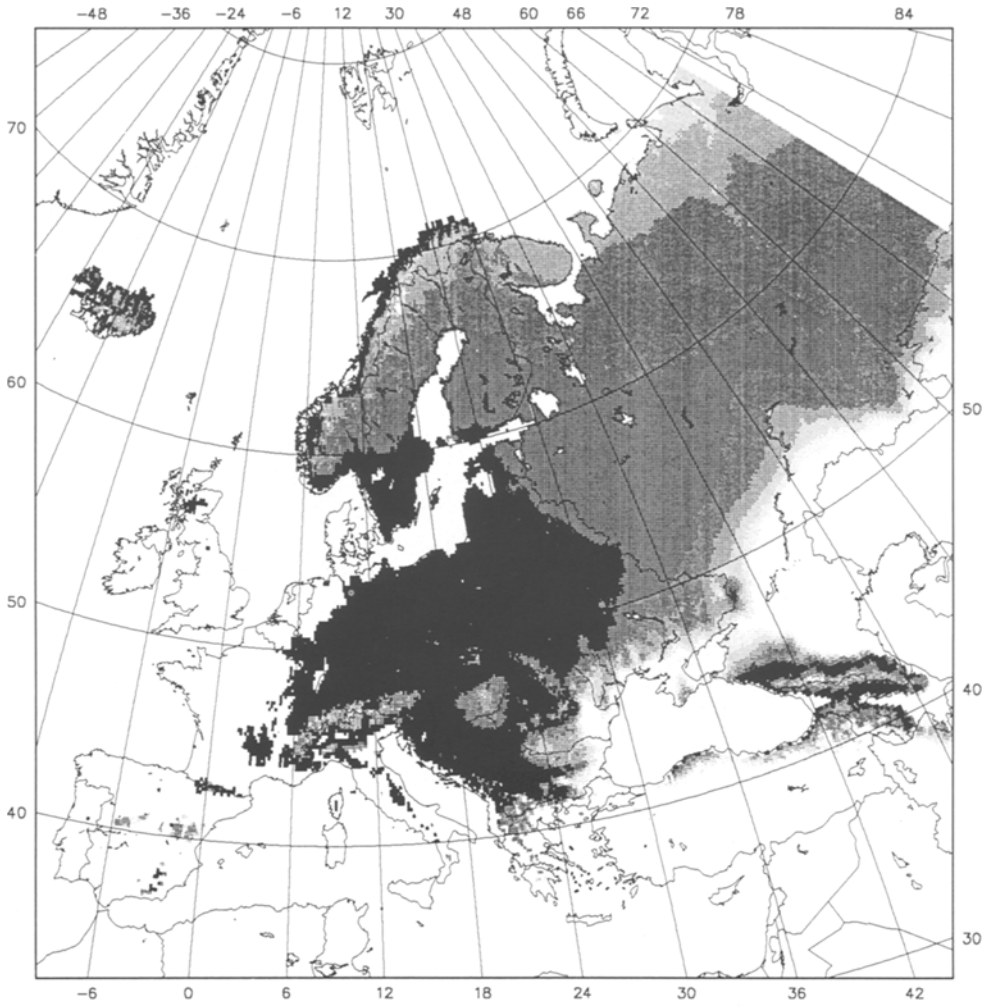


Fig. 1. (continued)



Populus tremula future climate

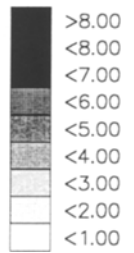
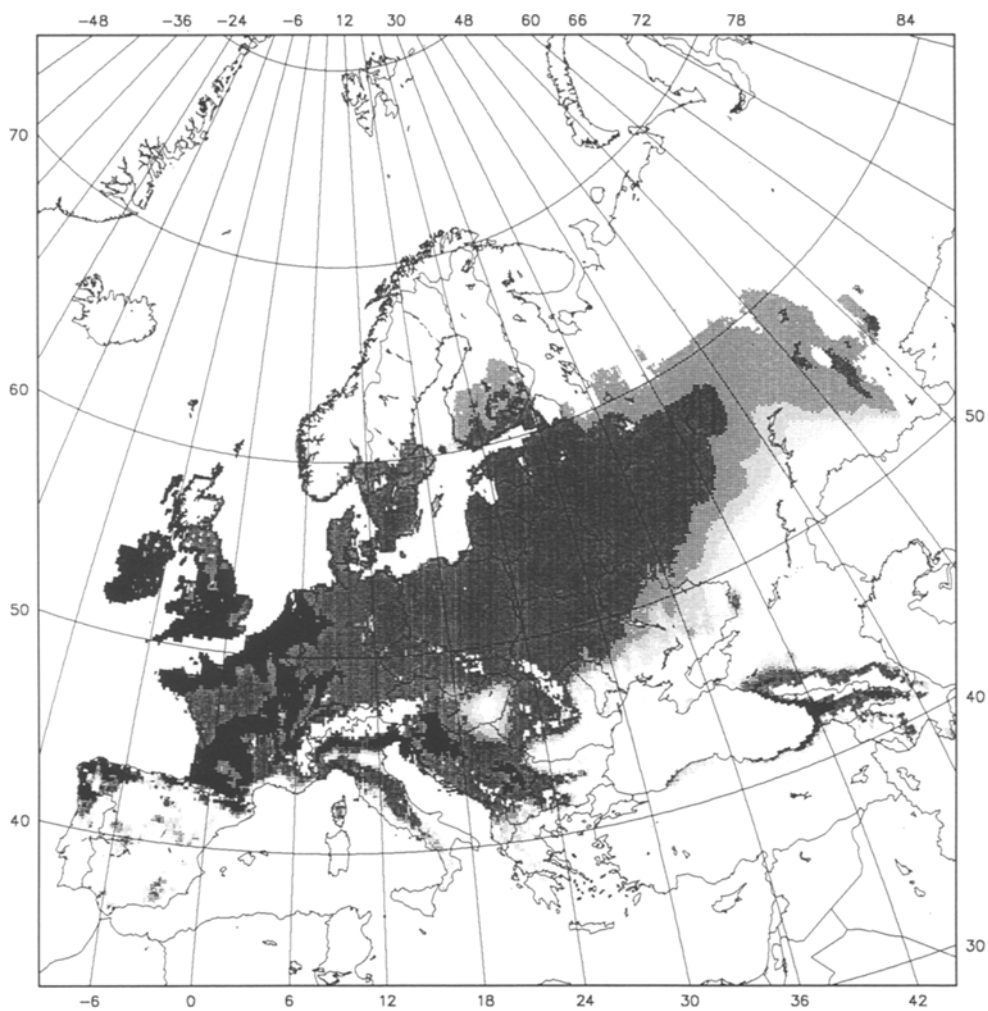


Fig.1. (continued)



Quercus robur

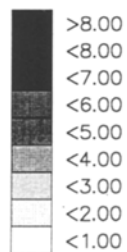
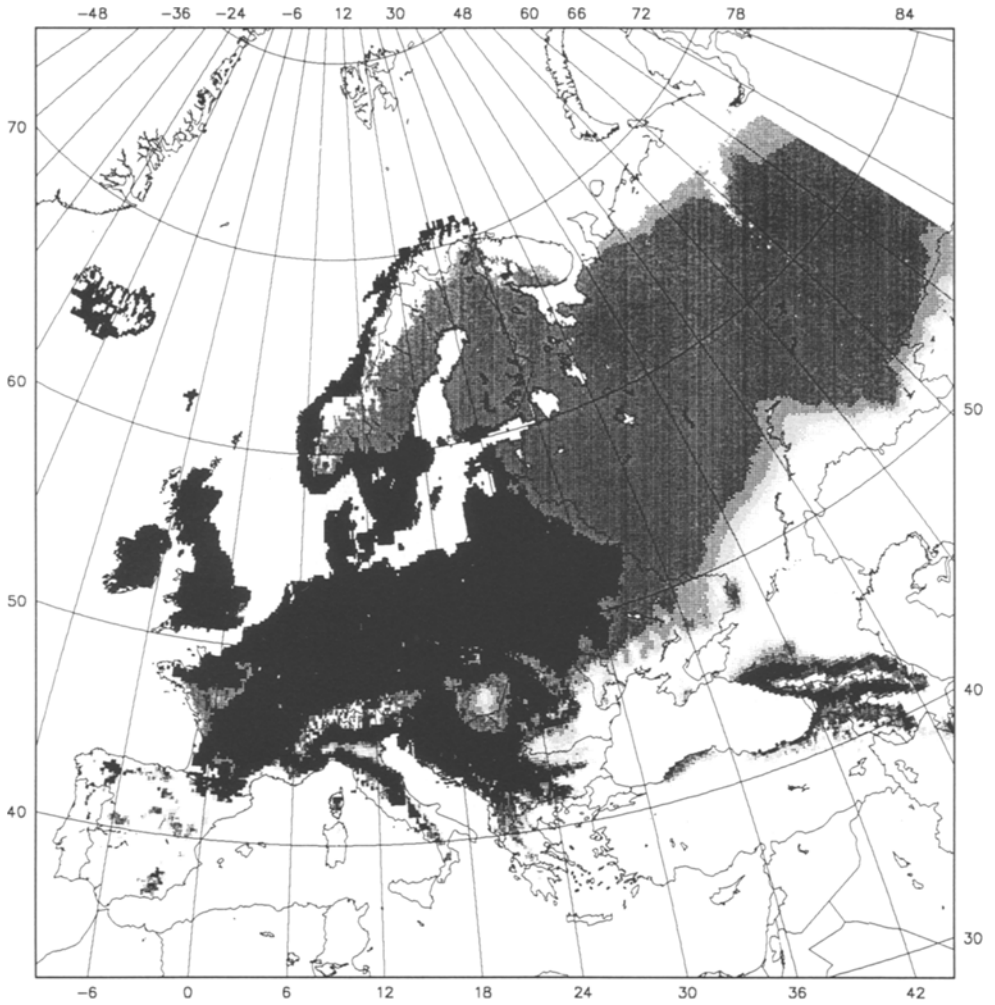


Fig.1. (continued)



Quercus robur future climate

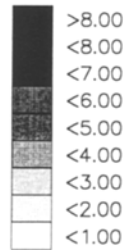
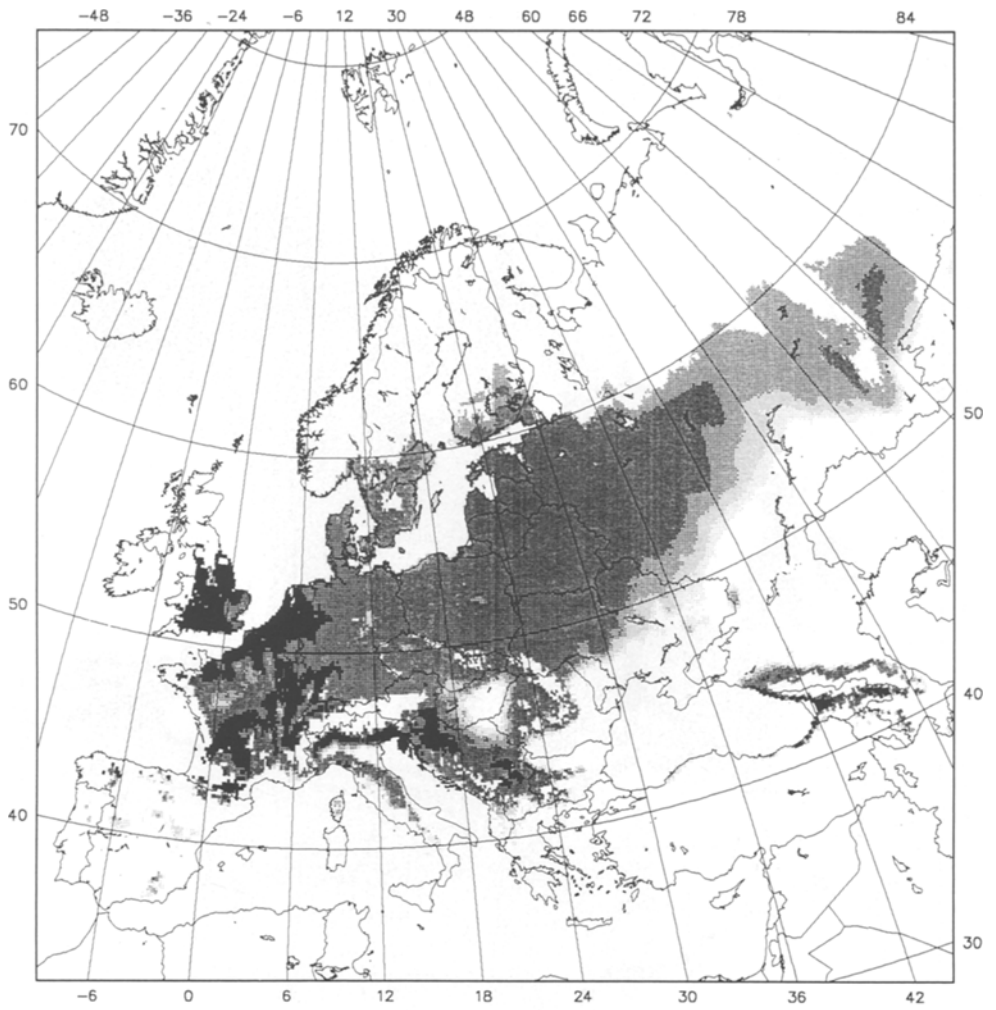


Fig. 1. (continued)



Tilia cordata

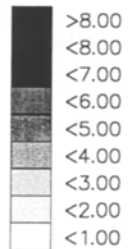
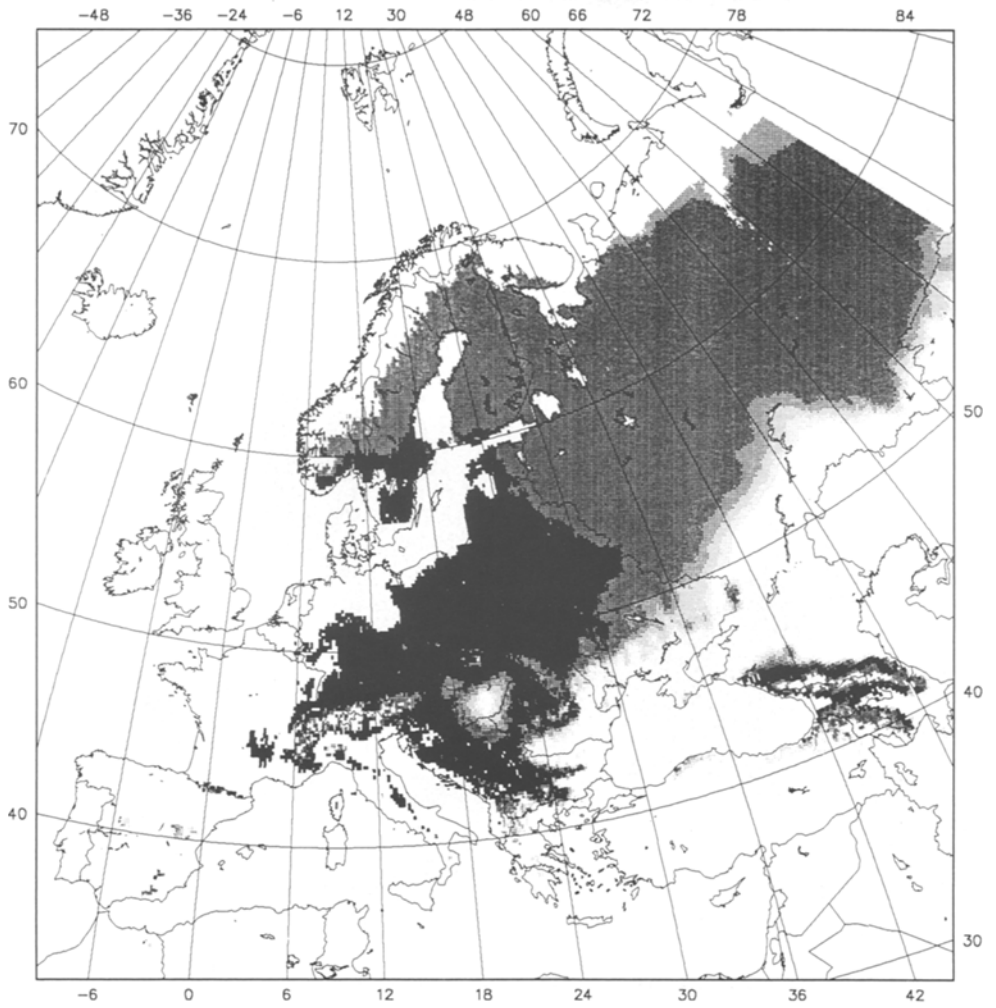


Fig.1. (continued)



Tilia cordata future climate

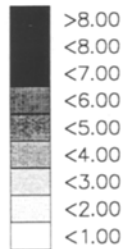
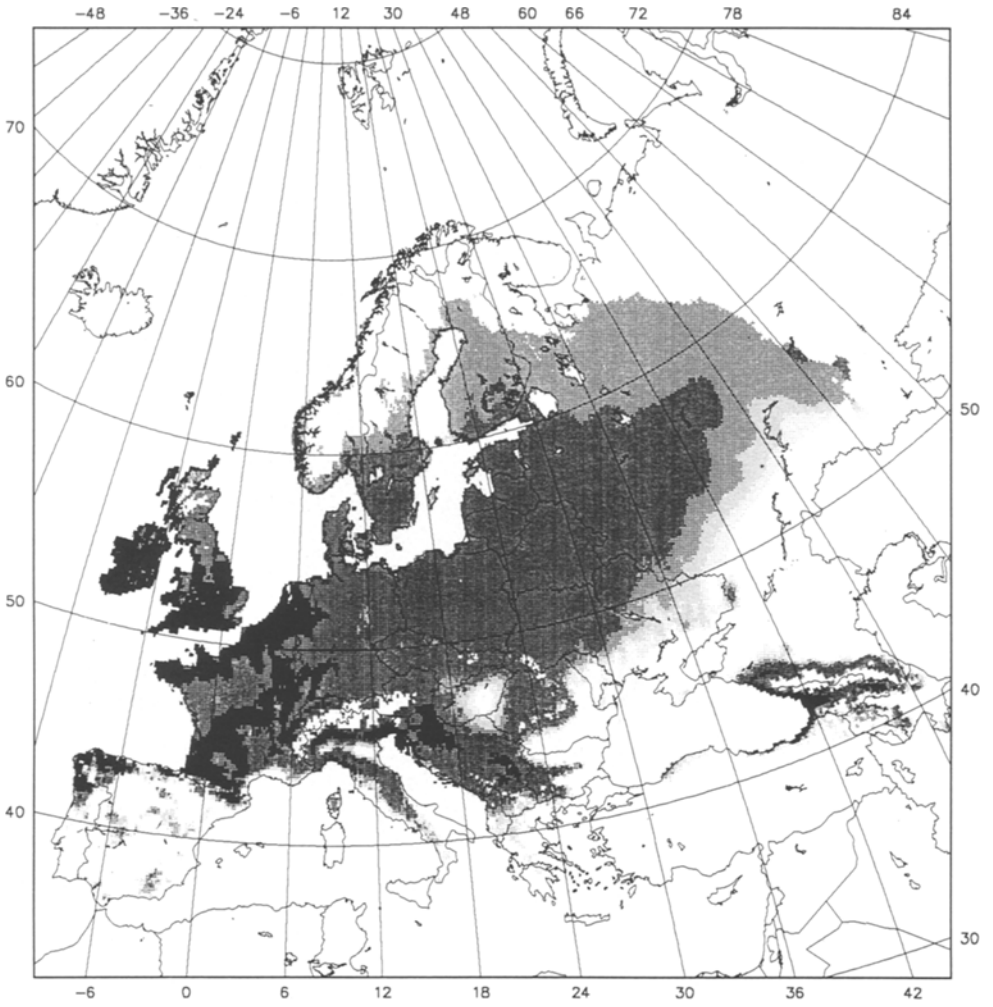


Fig.1. (continued)



Ulmus glabra

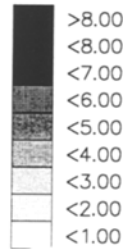
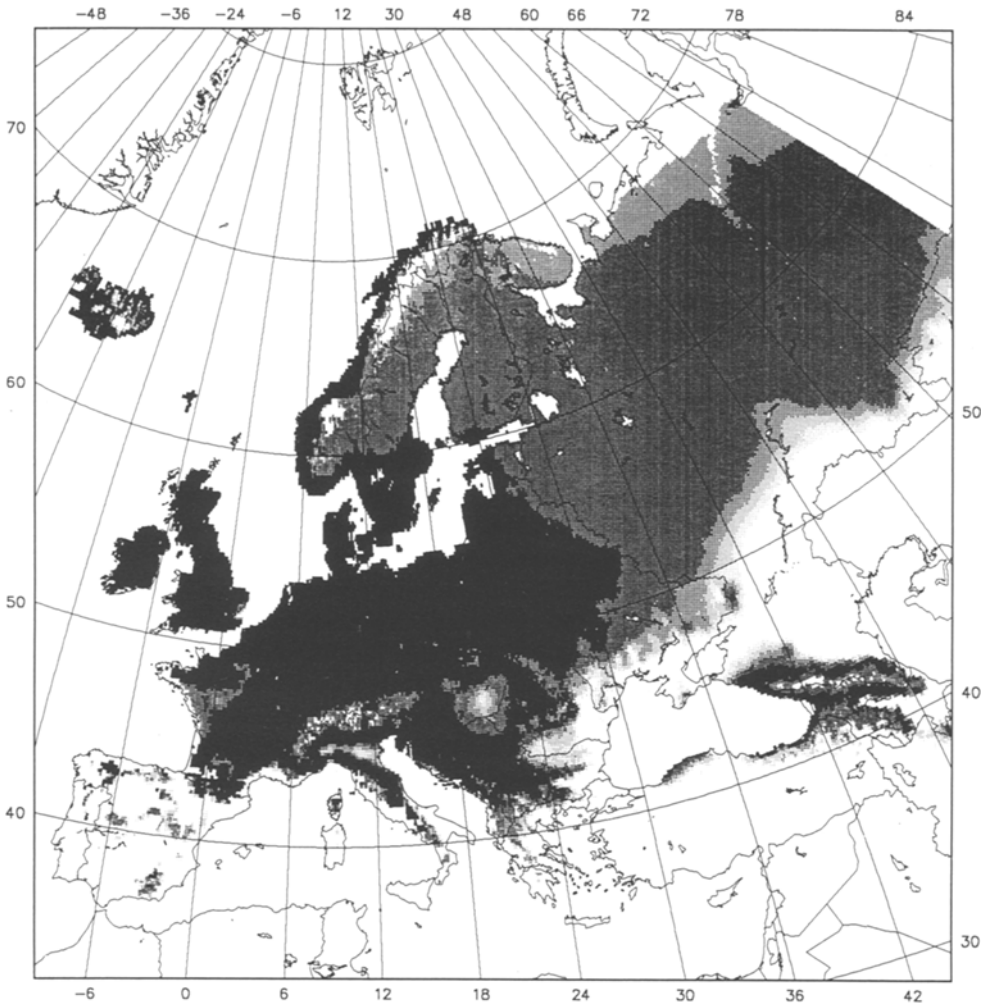


Fig.1. (continued)



Ulmus glabra future climate

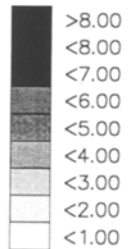


Fig. 1. (continued)

Ulmus glabra (Wych elm) is found throughout the southern and coastal central boreal zones (Figure 1). Under the changed climate it expands northwards to cover most of the boreal zone, except for some of the montane areas.

3.2. SPECIES DISTRIBUTION LIMIT CHANGES: COMMON TREES OF THE NEMORAL ZONE

Fagus sylvatica (beech). The northwestern distribution limit of *Fagus sylvatica* can be explained by its high chilling requirement (Figure 2). Without this adaptation to moderately continental conditions, *Fagus* would extend through Ireland and Scotland. Under the changed climate, *Fagus* extends a long way north into the boreal zone, while retreating from areas it at present occupies in the south and west.

Quercus petraea (sessile oak) occurs in part of southern Sweden, coastal Norway and Denmark (Figure 2). Under the changed climate its range is shown expanding to cover much of Fennoscandia, though it would be excluded from the western coastal fringes.

The degree and breadth of the possible changes in species ranges as described in these equilibrium simulations show the extent to which some the projections for climate changes in the boreal zone could dramatically alter the forest composition in northern latitudes. However, as these simulations are for equilibrium distributions, they give no information on the dynamics of change. Analysis of this is done at more local scale, using FORSKA2, as described in the following section.

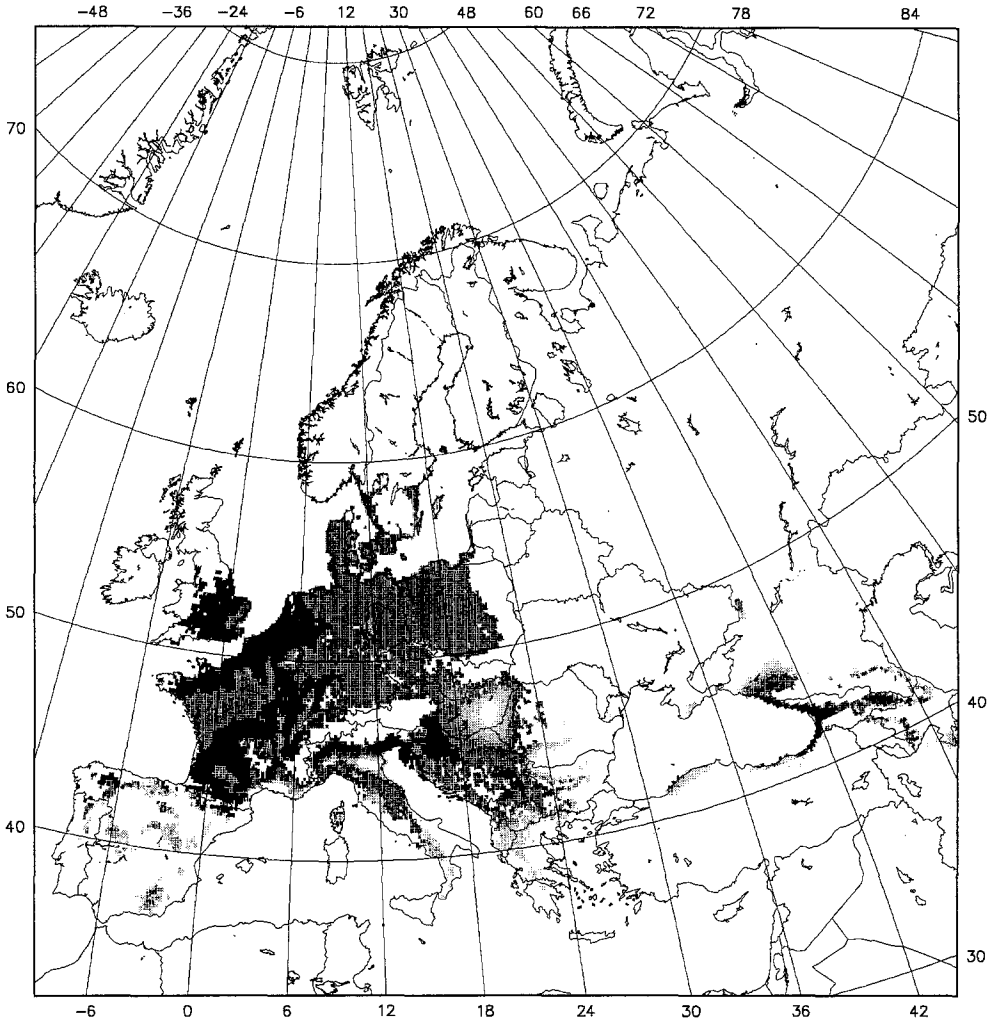
3.3. DYNAMIC SIMULATIONS

3.3.1. Reivo, Norrbotten

At this most northerly site (Figure 3), FORSKA2 simulates a typical Swedish boreal zone landscape in which *Picea abies* and *Pinus sylvestris* co-dominate (Figure 4a). Increased warming in the transient period initially favours both species equally. *Pinus*, however, in the longer term responds less favourably to the increased competition from *Picea* so that *Picea* comes to dominate. Boreal deciduous species also decline. Total biomass increases as *Picea* grows faster in response to warming.

3.3.2. Tandövala, Kopparberg

Tandövala lies in the boreal zone of central west Sweden (Figure 3) where the equilibrium vegetation in the present climate is again simulated as a *Picea*–*Pinus* forest (Figure 4b). During the transient period an increase in biomass occurs as *Picea* responds favourably to increased growing-season warmth. At the same time *Pinus* responds negatively to the increased competition from *Picea*. However, the warming continues beyond the limits for establishment of *Picea*, leading to local extinction within 250 yr. The major replacement is *Pinus sylvestris*. Here, as *Picea* declines, *Pinus* comes to dominate over new deciduous arrivals such as *Fagus sylvatica* (Figure 2). Forest composition changes dramatically from one climate phase to the next, but total site biomass seems to be little affected, even during the transient phase.



Fagus sylvatica

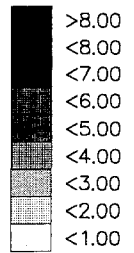
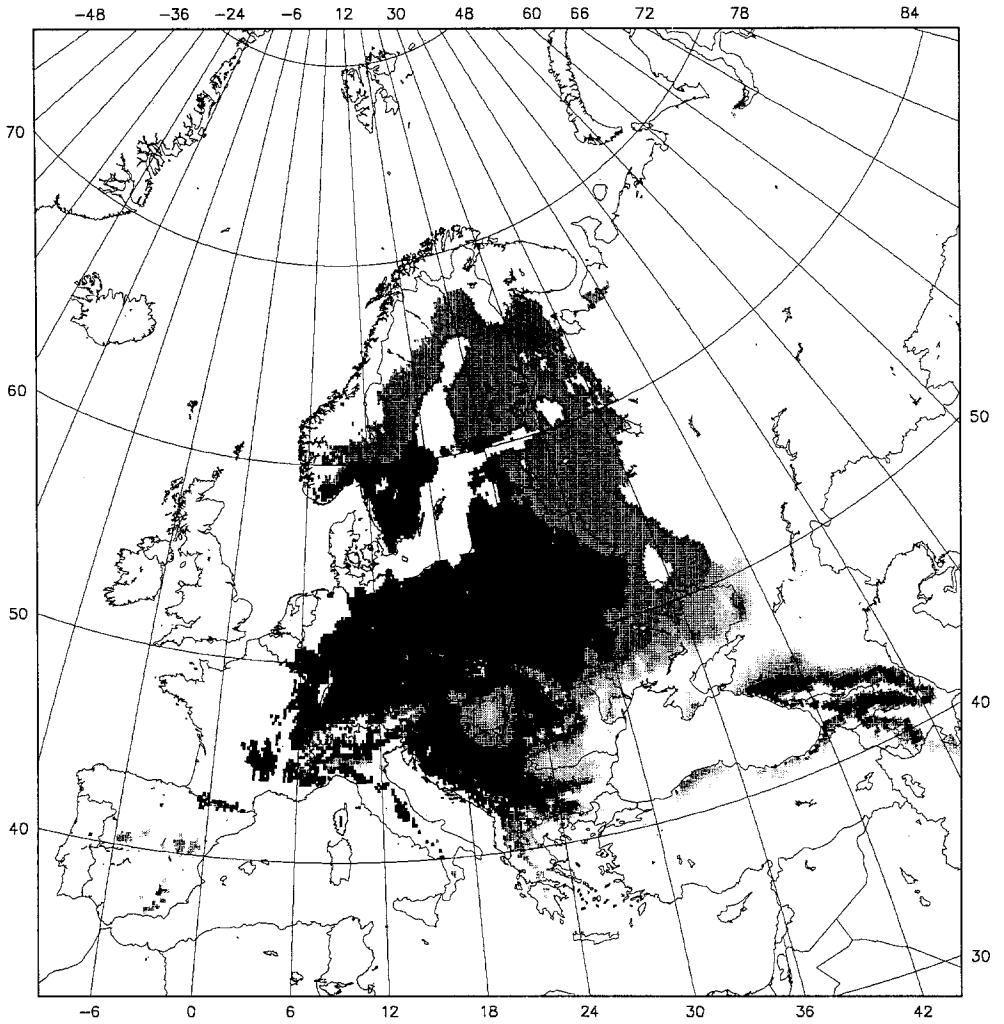


Fig. 2. Simulated distributions of two common nemoral zone trees from northern Europe under present and future climates (see Figure 1 for details).

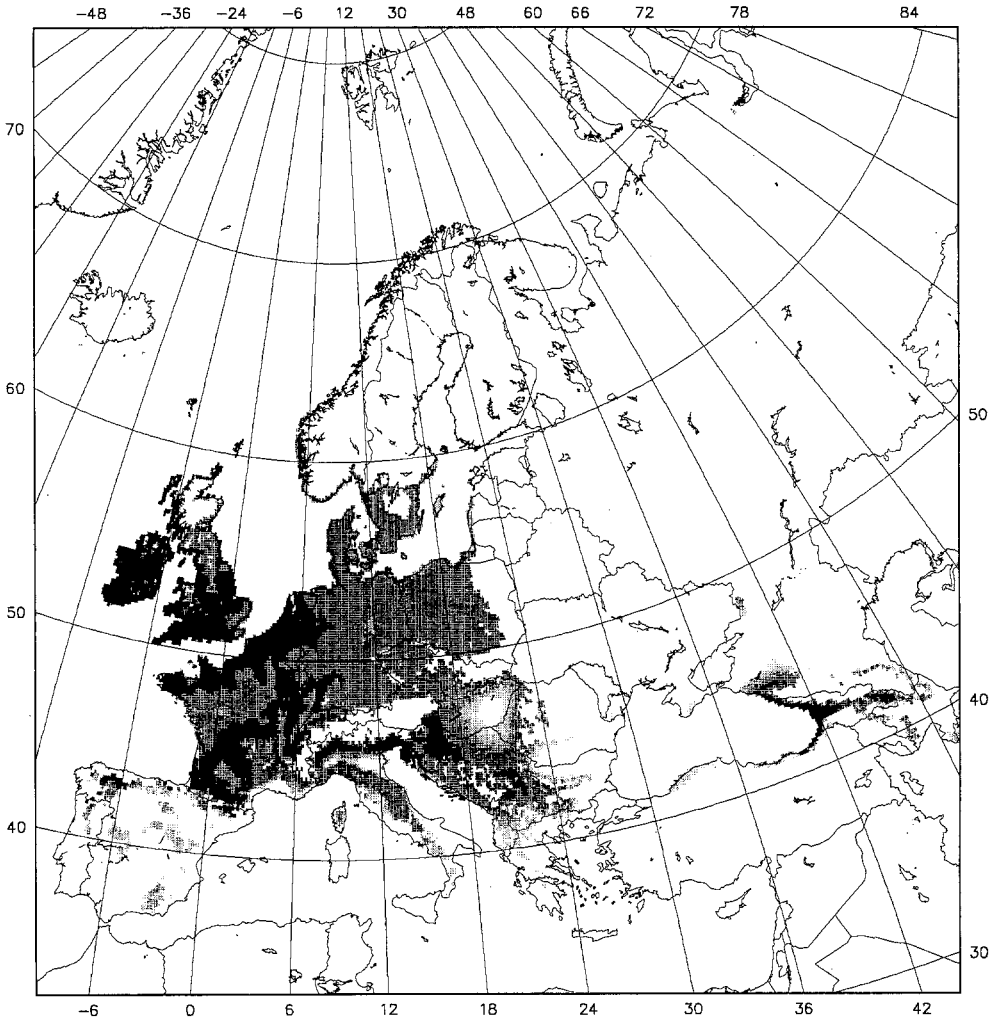
MODELLING TREE SPECIES RANGE LIMITS AND TRANSIENT RESPONSES



Fagus sylvatica future climate



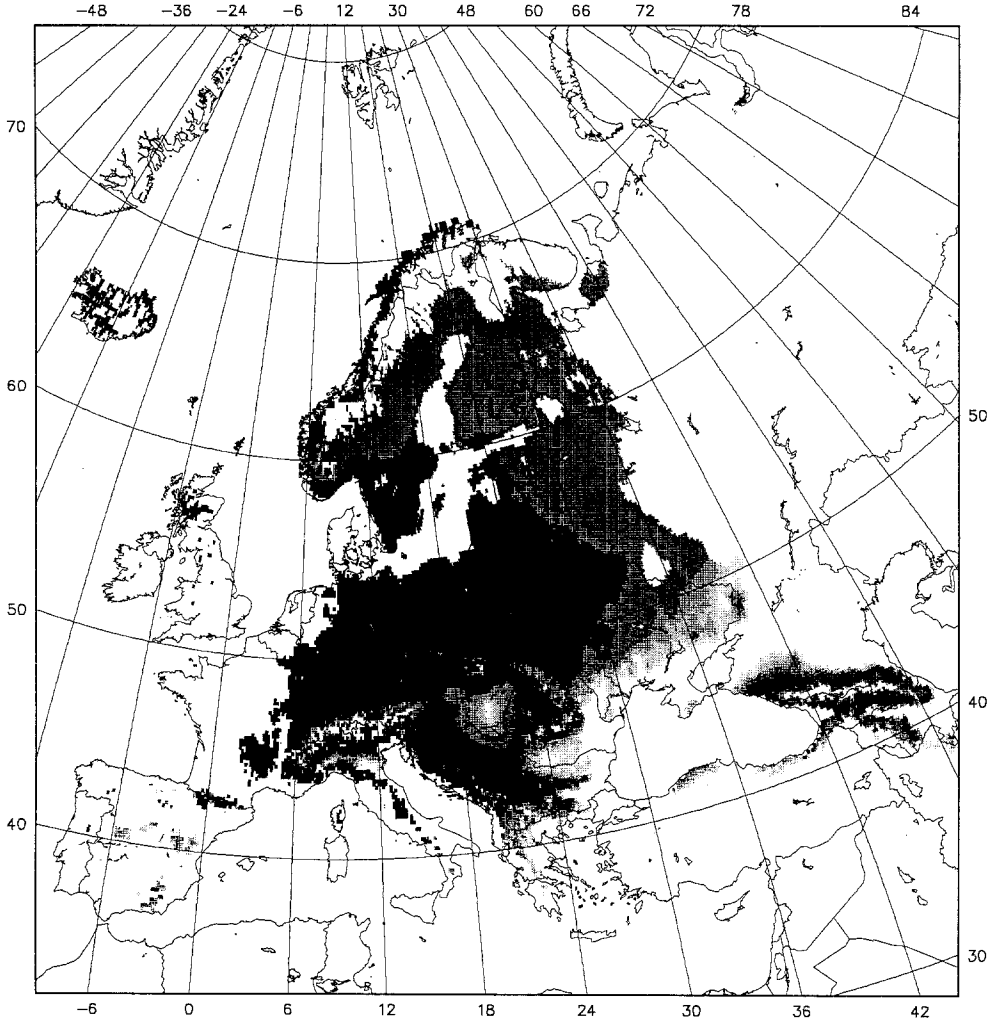
Fig. 2. (continued)



Quercus petraea



Fig. 2. (continued)



Quercus petraea future climate

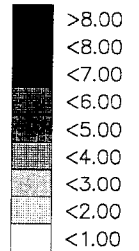


Fig.2. (continued)

3.3.3. Tyresta, Stockholm

Tyresta lies in the boreo-nemoral zone of central Sweden. Today *Picea* and *Pinus* dominate (Figure 4c), but a number of deciduous species (including *Betula* and *Quercus* spp.) also contribute significantly to the total biomass. The warming phase leads to a rapid decline of the conifers, as well as a brief decline in biomass and a corresponding increase in the deciduous species already on site. The major component of the new forest however is *Fagus sylvatica*, which was not originally present. Biomass increases, a substantial part of this increase being due to *Fagus*.

However if no immigration of new species is allowed, the forest composition under the new climate becomes dominated by *Quercus* and *Betula* spp. (Figure 7). Biomass then declines rapidly during the transient phase, recovering only after ≈ 150 yr to a level slightly less than would be achieved in the presence of *Fagus*.

3.3.4. Tiveden, Örebro

Picea is dominant in the simulation of this region (Figure 4e), though *Pinus* forms quite a large part of the biomass. Deciduous species are present though in minor amounts. *Picea* declines rapidly in the transient phase, as new recruitment fails, and



Fig. 3. Locations of the five sample sites.

Pinus is outcompeted by the increasing presence of deciduous species. *Fagus* immigrates and becomes the dominant species. Here, however, there is somewhat less biomass under the changed climate than was shown for the present climate.

3.3.5. *Boa Berg, Halland*

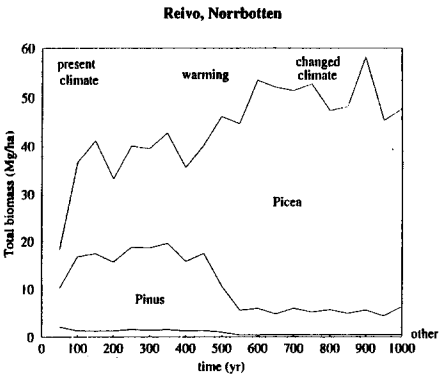
This site lies near the border between the boreo-nemoral and nemoral zones (Figure 3). *Picea* is still the major component but *Pinus* and some deciduous species, including *Fagus*, make up the rest of the forest (Figure 4f). Once the warming begins there is a complex transitional response in which *Picea* and *Pinus* decline rapidly but *Pinus* remains in the forest (in small amounts) even under the new warmer climate. *Fagus* increases during the transient phase, only to decline abruptly later due to failure of chilling. *Fagus* is then replaced by a *Betula-Quercus* forest of lower biomass than before the warming began.

4. Discussion and Conclusions

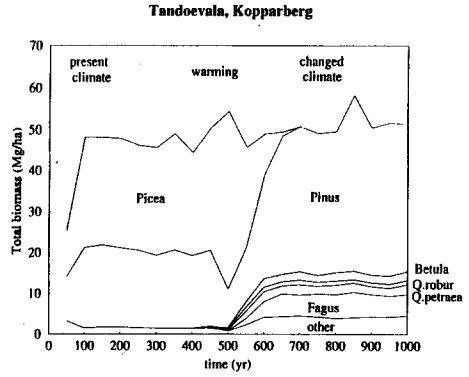
The models predict large changes in the boreal and boreo-nemoral forests of northern Europe. STASH, as a static model, predicts these changes by modelling present and potential equilibrium ranges of species over large regions. STASH also calculates a rough index of the potential productivity of each species. Some boreal species (e.g. *Picea abies*) are more productive in the warmer areas of their ranges than in colder. There is no decline in productivity towards the southern boundary. These observations, reproduced by STASH, run counter to the parabolic response curve to GDD as used in early forest gap models (Botkin *et al.*, 1972). There is no basis for a maximum GDD limit (Prentice *et al.*, 1991; Prentice *et al.*, 1993; Sykes *et al.*, in press). However the boreal conifers do show abrupt southern and western limits which may be explained by other mechanisms including chilling requirements and increasing competition from deciduous species. Our models embody reasonable hypotheses about these limits, but more experimental work on the mechanisms is needed in order to reduce the associated uncertainties.

Many boreal species show range shifts under the changed climate scenario. These changes are of such a magnitude as to give a completely different structural and compositional character to much of landscape now occupied by boreal or boreo-nemoral forest. The true boreal forest of Fennoscandia may after a climate change become restricted to the far north and the mountains.

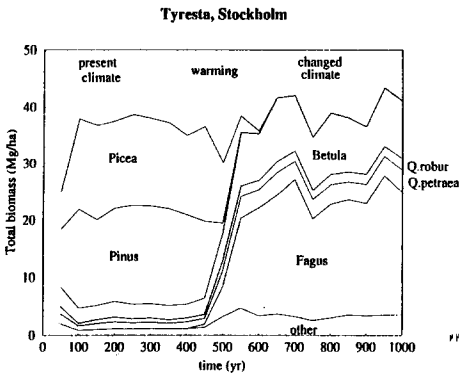
The forest gap model approach using FORSKA2 indicates some of the possible routes that different regions might follow in response to a changing climate. Forest dynamics simulated at five representative sites show a variety of behaviour. The speed of the changes can be strongly influenced by the future disturbance and management regimes as well as by an interaction with species availability (Sykes and Prentice, unpubl. ms.). In the north, species already in the forest may respond favourably to a warmer climate. Further south there is a greater potential for loss of current species and the possibility of immigration for warmth-requiring deciduous species. Natural immigration may take some time. Simulations for Tyresta, with immigration suppressed, show that there is at least a possibility that species already in the region



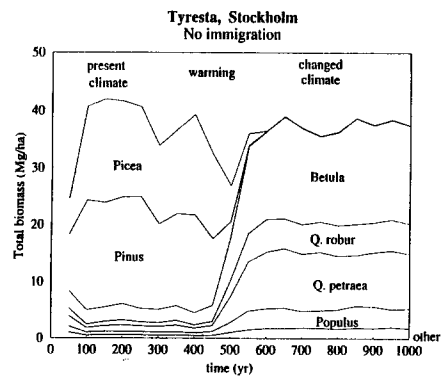
(a) Near Reivo, Norrbotten, northern Sweden.



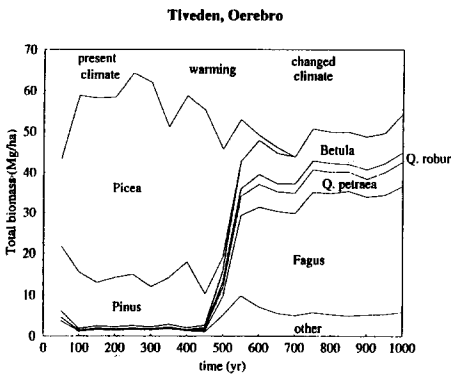
(b) Near Tandövala, Kopparberg, north-central Sweden.



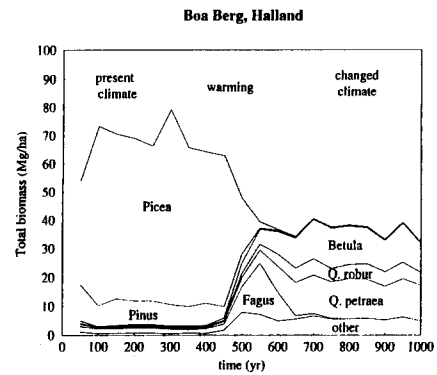
(c) Near Tyresta, Stockholm, central-south Sweden.



(d) as (c), but only those species present in the region under the *current* climate were available for establishment in the future.



(e) Near Tiveden, Örebro, southern Sweden.



(f) Near Boa Berg, Halland, southwestern Sweden

Fig. 4. Simulation of forest landscape at the five sites in Sweden shown in Figure 3. A linear change in climate was imposed during the 100 year period marked "warming". After that, the climate remained constant at the mean $2\times\text{CO}_2$ climate for each location.

could maintain the previous biomass despite a major change in dominance. Further south, where we have not considered the possibility that still more warmth-demanding species might invade, the existing species will not maintain present biomass in the changed climate, so there could be substantial net losses of forest biomass. Such effects could be mitigated by importing and planting species from other regions. The example of *Fagus*' behaviour in the Boa Berg simulation illustrates the potential for surprise in this approach. Managing forests under climate change will be risky, unless climate can be reliably projected 100 yr ahead.

Both modelling approaches have been used to give some indications of the possible changes that could occur in the north European boreal forest. The two models provide us with different but complementary insights into how species respond to climate in general, and how the potential effects of climate change in these northerly regions could affect forest landscapes. The picture they give is presumably incomplete and disregards (among many other things) the direct physiological effects of changed CO₂ that would be expected to modify several aspects of the tree species' response. Nevertheless, the models indicate quite drastic changes due to climate acting through basic mechanisms that will continue to operate, regardless of further modifying factors, and which imply major consequences for the future of both natural and managed forests.

Acknowledgment

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