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Abstract. It is hypothesized that the principal features of higher plant distributions at continental scales are determined by the macroclimate. Bioclimate data have been computed on a 50 km grid across Europe. Along with published maps of higher plant distributions based upon the same grid, these data have been used to derive climate response surfaces that model the relationship between a species' distribution and the present climate. Eight species representative of a variety of phytogeographic patterns have been investigated. The results support the hypothesis that the European distributions of all eight species are principally determined by macroclimate and illustrate the nature of the climatic constraints upon each species. Simulated future distributions in equilibrium with $2 \times CO_2$ climate scenarios derived from two alternative GCMs show that all of the species are likely to experience major shifts in their *potential* range if such climatic changes take place. Some species may suffer substantial range and population reductions and others may face the threat of extinction. The rate of the forecast climate changes is such that few, if any, species may be able to maintain their ranges in equilibrium with the changing climate. In consequence, the transient impacts upon ecosystems will be varied but often may lead to a period of dominance by opportunist, early-successional species. Our simulations of potential ranges take no account of such factors as photoperiod or the direct effects of CO_2, both of which may substantially alter the realized future equilibrium.

Key words. Climate response surfaces, global change, phytogeography, conservation

INTRODUCTION

Biogeographers have long recognized the fundamental role of macroclimate in determining the distribution patterns of many organisms at scales of 10^2 km and above. Plant geographers have developed explicit models that relate physiognomically-defined vegetation units to climate (Holdridge, 1947, 1964; Walter, 1979) and, more recently, have related the occurrence of plant functional types to threshold values of a small number of bioclimate variables (Box, 1981; Prentice *et al.*, 1992). The geographic range limits of individual plant species also have been related to macroclimate constraints (Pigott & Huntley, 1981) although, as the work of Hintikka (1963) demonstrated, there frequently is an interaction between two or more climate variables with respect to their threshold values.

Studies such as those of Hintikka (1963) and Iversen (1944) employed a re-mapping of the species' distribution into a 'climate space' whose axes corresponded to two or more climate variables. In both cases, these authors used meteorological stations as the localities and recorded the presence or absence of the species of interest in the proximity of each station. The re-mapping then utilized the climate data from the stations directly. As an alternative to this approach, meteorological station data may be interpolated to provide estimates of climate conditions at all of a series of localities where a species is recorded. Until recently, the principal limitation of methods for interpolation of meteorological data related to the problems posed by orographic climatic gradients, rendering this approach of limited value in topographically diverse regions. Hutchinson (1989), however, has developed a technique that enables elevation-sensitive interpolations to be made of the climate at any locality using data from meteorological stations in the surrounding region. Using this technique, Nix & Switzer (1991) have interpolated the climate conditions for individual localities from which vertebrates have been recorded in Australia and have used these data to define bioclimatic envelopes for the species. Mitchell (1991) has employed this approach to investigate the climatic determinants of the range of *Agathis australis* Steud. (Kauri) in New Zealand.

Bartlein, Prentice & Webb (1986) proposed the method of 'climate response surfaces' as a means for quantitatively relating the abundance of particular pollen taxa in contemporary surface samples to climate conditions at the localities from which the samples were collected. Gignac *et al.* (1991a,b) employed a very similar approach when they fitted response surfaces for individual bryophyte species with respect to a variety of environmental gradients; the surfaces describing, in this case, how the percentage cover values for the bryophyte species varied across the environmental space.

Palaeoecologists have demonstrated that, as Good (1931) proposed, the fundamental response of terrestrial organisms to environmental change is one of migration (Davis, 1976; Huntley & Webb, 1989; Huntley, 1991). This migratory response serves to maintain species' ranges in a dynamic equilibrium with their environmental constraints. Given the likelihood of substantial climate changes in the near future as a consequence of anthropogenic emissions of radiatively active gases ('greenhouse gases') into the atmosphere (Houghton, Jenkins & Ephraums, 1990; Houghton, Callander & Varney, 1992) it is likely that many species will exhibit a tendency to shift their range limits in response to the changing climate conditions experienced (Overpeck & Bartlein, 1989; Cramer & Leemans, 1993; Huntley, 1995).

The geographical distributions of many individual species have been mapped for various regions ranging from individual counties of England to the globe. However, these maps generally portray only qualitative information about the presence or absence of the species in any given geographical location. Furthermore, many of the published maps are only relatively imprecise maps of the overall extent of a species' range, conveying no information about the relative continuity of the species' occurrence within this limit. Notwithstanding these limitations, published distribution maps represent an invaluable source of data that may be used to investigate the climatic determinants of species' distributions. Carey & Ullyett (1993) used a multiple regression approach to relate the present distribution of *Himantoglossum hircinum* (L.) Sprengel (Lizard Orchid) in Britain to climate. They then used this relationship to attempt to forecast the potential future distribution of the species given a particular climate change scenario. Unfortunately, whereas the species distribution was recorded as presence or absence on both a 1 km and a 10 km grid, the climate data available to them were related to a 40 km grid, limiting the precision of the relationship that they were able to obtain between climate and the species' occurrence. They overcame this limitation to some extent by relating the number of recorded localities for the species within each 40 km square to the climate of the latter; this relationship was then used to predict the potential future number of localities in each 40 km square under the changed climate scenario.

A variety of other approaches have been adopted by various workers seeking to relate the distributions of organisms to environmental gradients, including Gaussian response models, logistic regression, generalized linear and/or additive models, etc. (Ter Braak & Looman, 1986; Austin, 1987; Ter Braak 1987; Yee & Mitchell, 1991). Overpeck & Bartlein (1989) predicted the likely impact of 21st century climate change upon the forests of North America using pollen-climate response surfaces. The response surfaces were derived from contemporary climatic data and relative abundance values of pollen taxa in surface samples and were fitted using locally-weighted regression (Cleveland & Devlin, 1988). Subsequently, P. J. Bartlein (pers. comm.) developed a technique for fitting probability response surfaces using gridded presence-absence data describing species' current distributions. This approach depends upon the availability of species' distribution data and climate data for the same grid. It utilizes a similar approach to that used in fitting pollen-climate response surfaces (Bartlein *et al.*, 1986; Huntley, Bartlein & Prentice, 1989; Huntley, 1992, 1993) but the surface now describes the probability of the species' occurring at a given point in climate space.

We have used Bartlein's presence-absence response surface methodology (P. J. Bartlein, unpublished computer programs), with some modifications, and have applied this approach to species' distribution and climate data related to the *c.* 50 km UTM grid used in *Atlas Florae Europaeae* (Jalas & Suominen, 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991). The resulting response surfaces, fitted with respect to three bioclimate variables, are illustrated for eight selected species. The surfaces then are used to simulate the potential future distributions of these species for two alternative climate scenarios for radiative forcing equivalent to a doubling of pre-industrial atmospheric carbon dioxide concentrations. These scenarios are obtained from two general circulation model (GCM) simulations made using the United Kingdom Meteorological Office (UKMO) (Mitchell, 1983) and Oregon State University (OSU) (Schlesinger & Zhao, 1989) models respectively. These two GCM simulations are representative of high (UKMO) and low (OSU) sensitivity model results and the two scenarios may thus be considered to be representative of the range of possible outcomes of climate change during the next century.

The simulated distributions illustrate a range of responses amongst the eight species chosen. For many of the species, the magnitude of the changes in range that are simulated represents range-limit shifts that will take many centuries, if not millennia, to achieve given palaeoecological evidence of past migration rates (Davis, 1976, 1981, 1983; Huntley & Birks, 1983; Huntley, 1988; Birks, 1989; Huntley, 1989). Furthermore, for some relatively restricted species the future range may largely not coincide with the present range, raising doubts as to the capability of the species' to survive the forecast environmental changes.

METHODS

Capturing species distributions

The European distributions of >2000 higher plants have been published as presence-absence maps using a *c.* 50 km UTM grid in *Atlas Florae Europaeae* (AFE) (Jalas & Suominen, 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991). These data represent the single most extensive systematic mapping of European higher plants, whilst the use of the 50 km UTM grid offers the advantage of an almost equal area mapping unit across the considerable latitudinal extent of the biogeographic province of Europe that extends from Crete ($<35°$ N) to Svalbard ($>80°$ N). Although the species mapped to-date represent only *c*.15% of the flora of Europe, they include most of the trees and shrubs as well as several major families dominated by herbaceous species.

We have adopted the grid defined in AFE and have captured distributions recorded upon this grid manually in machine-readable form. We also have collaborated with T. Lahti in Helsinki who has developed a scanning approach to capture machine-readable distributions from the original AFE maps held in the Helsinki Museum (T. Lahti, unpublished results).

In the case of species that we wished to investigate but that have yet to be mapped by AFE, we have used other sources of distribution maps and have manually transcribed the species' distributions onto the AFE grid to produce facsimiles of AFE maps for these species. These have then been captured in machine-readable form using the manual procedure that we have developed.

The AFE grid, as originally published (Jalas & Suominen, 1972), comprises 4419 cells. The longitude and latitude of the centre and corners of each of these have been computed in collaboration with M. O. Hill (unpublished), allowing the AFE grid to be related to other datasets in which positions are defined in terms of longitude and latitude.

Environmental data

The principal environmental data required for our investigation were climate data. However, given the considerable relief in many parts of Europe and the consequent need to take elevation into account when interpolating climate data between the available meteorological stations, an elevation dataset was also required. The 10′ resolution global elevation dataset compiled by the Fleet Numerical Oceanography Center (Cuming & Hawkins, 1981) and distributed on CD-ROM by the USDOC/NOAA National Geophysical Data Center (NOAA-EPA Global Ecosystems Database Project, 1992) was the primary source used. This dataset gives the minimum, maximum and modal elevation for each 10′ longitude-latitude pixel classified as land. We have computed the 'mean' elevation for each AFE grid cell as a weighted mean of the modal elevations of all of those 10′ pixels partially or completely enclosed by the AFE cell. The weights used were the areas of each pixel that were within the AFE cell boundaries. The resulting 'mean' elevations were each based upon an average of >20 modal elevations for 10′ pixels.

We also have estimated the minimum and maximum elevation for each AFE cell as the minimum and maximum of the minima and maxima respectively of all those 10′ pixels that had at least 50% of their area within the AFE cell. These extreme values each were based upon an average of >12 such values for 10′ pixels.

Of the 4419 cells, fifteen did not enclose part(s) of any 10′ pixel(s) classified as land and a further six enclosed less than 0.5 of the area of a single pixel classified as land. These twenty-one cells were identified and their locations examined; they showed concentrations in the Mediterranean, around the Åland archipelago in the Baltic and to a lesser extent around Svalbard. All proved to represent small islands; their mean, maximum and minimum elevations were assigned following visual inspection of available maps. The completed dataset was mapped (Fig. 1).

The primary climate dataset used was a compilation of meteorological station data made initially by Leemans & Cramer (1991) and subsequently considerably enlarged by WC. These data principally relate to the climate normal period 1931–60 and comprise mean monthly values, of which those for temperature, precipitation and cloudiness were used in this study. Some of the station records utilized are for periods of less than the full 30-year normal period; these are used in regions where data are otherwise sparse and are especially valuable with respect to precipitation because this shows greater regional variability. Monthly temperature, precipitation and cloudiness data were available from 4242, 7225 and 1141 stations respectively within the overall geographical area under consideration.

The station data were interpolated to locations at the geographical mid-point and mean elevation of each AFE cell. Interpolations were performed by means of Laplacian thin-plate spline surfaces fitted to the station data (Hutchinson, 1989). The independent variables for these surfaces were the longitude, latitude and elevation of the stations. Separate surfaces were fitted for each of the thirty-six meteorological variables used. Because of the geographical extent and topographical complexity of Europe it was necessary to fit spline surfaces for a series of separate overlapping geographical windows; the high density of meteorological stations available made this possible. The mean numbers of stations per window were 709, 1125 and 302 for temperature, precipitation and cloudiness respectively, with minima and maxima of 116/1519, 95/2995 and 105/658.

Although in previous studies response surfaces for pollen taxa and/or higher plants have been fitted with respect to conventional meteorological variables (e.g. mean temperatures of January and July (Huntley *et al*., 1989); mean temperatures of January and July plus mean annual precipitation (Bartlein *et al*., 1986; Prentice, Bartlein & Webb, 1991; Huntley, 1992, 1993)) these generally have been presented as surrogates for variables having more direct physiological mechanistic roles in limiting the ability of plants to survive and grow. Prentice *et al*. (1992) presented a global biome model in which five 'bioclimate' variables were used to determine the occurrence of a series of plant functional types that in turn combined in various ways to define biomes. We used the same bioclimatic procedure to estimate the five bioclimate variables for each AFE grid cell using the interpolated meteorological variable values.

In order to estimate the index of moisture availability used by Prentice *et al*. (1992), namely the ratio of actual to potential evapo-transpiration, it is necessary to know the soil water capacity. We used the same 0.5° resolution global dataset of soil water capacities as Prentice *et al*. (1992) and the same procedure as for the elevation data to

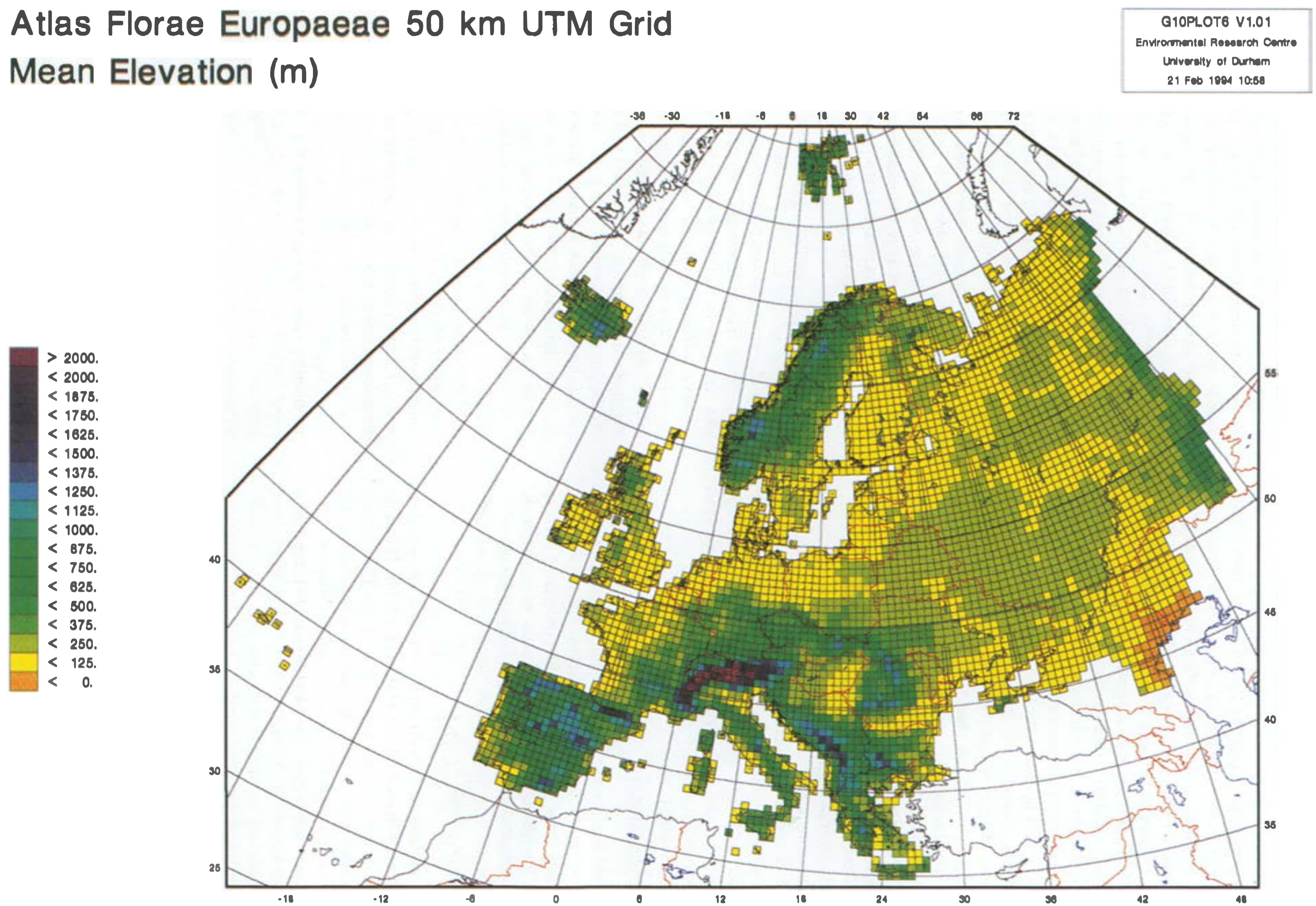

FIG. 1. Mean elevation of each AFE grid cell.

obtain mean soil water capacity values for each of the AFE cells. In the case of cells classified as ocean in the topographic dataset (see above) a default water capacity value (150 mm) was assigned.

Two of the variables used by Prentice *et al.* (1992) were of less relevance in the context of Europe. Minimum values of 22°C for the mean temperature of the warmest month (MTWA) and of 100 degree days for the temperature sum above a 0°C threshold (GDD0) each defined limits for the occurrence of two non-tree functional types of warm/hot and cold environments respectively. Although 722 (16.4%) of the AFE cells have MTWA values >22°C, few of these also have sufficiently low values of the ratio of actual to potential evapotranspiration for this to be relevant in terms of the criteria presented by Prentice *et al.* (1992). Only fifty-seven (1.3%) of the AFE cells have GDD0 values <104. Given the limited penetration of their thresholds into our region, it would be biologically, as well as statistically, inappropriate to fit these two variables as response variables. We therefore elected to fit response surfaces in the three-dimensional climate space defined by the other three bioclimate variables of Prentice *et al.* (1992), namely the mean temperature of the coldest month (MTCO), the temperature sum above a 5°C threshold (GDD5) and an estimate of the ratio of actual to potential evapotranspiration (AET/PET). Of the threshold values used by Prentice *et al.* (1992), seven of eleven for MTCO, all five for GDD5 and eleven of twelve for AET/PET fell within the range of values computed for the AFE cells. Whereas the omission of the GDD0 threshold may result in an inability to correctly predict the limit of some herbaceous species in e.g. Svalbard, the omission of the MTWA threshold might cause problems in correctly modelling the limit of some south European shrub or herb species. However, in the present study none of the species comes into this latter category. The three bioclimate variables used to fit the response surfaces have been mapped (Figs 2–4).

Climate response surfaces

Response surfaces have been fitted using the species presence or absence in each of the 4419 AFE grid cells and the three bioclimate values estimated for each cell as described above; no distinction has been made amongst the various categories of record for a species distinguished by AFE. The surfaces are fitted by locally-weighted regression (Cleveland & Devlin, 1988) and the fitted values express the probability of the species occurring at a given location in the climate space. Fitted values have been evaluated using a $40 \times 40 \times 40$ grid of 'nodes' in the climate space. The intervals between grid points along the three climate axes are 1.0°C (MTCO), 130 degree days (GDD5) and 0.025 (AET/PET). Fitting uses a tricube weighted average of 'occurrence' (Huntley *et al.*, 1989) within a window around each grid point; the window widths used are 3.0°C, 300 degree days and 0.1 respectively.

No further smoothing or extrapolation of the fitted surfaces has been performed. Although further smoothing renders the surfaces visually simpler to comprehend and may also seem inherently reasonable, given conventional ecological models of species response along environmental gradients, it has the major disadvantage that it is liable to render the margins of the range less distinct. Surfaces that have been smoothed too much are thus less able to simulate the observed species' distribution and consequently are less useful from our point of view. Furthermore, given that the fitted surface represents the 'realized' distribution of the species as determined not only by its own inherent responses to the environmental gradients but also as the outcome of interactions with numerous other species, each of which is responding in an individualistic manner to these and possibly other gradients, it is likely that it is inherently rough. The conventional 'smooth' model of species' response along ecological gradients relates to a 'fundamental' property of the species that may rarely be expressed in nature.

The response surfaces are illustrated as a series of eight slices through the third bioclimate axis (AET/PET) using a program written for the purpose. The probability of occurrence of the species is represented by differential shading and the surface is portrayed as a 'mosaic' with each tile representing a node on the $40 \times 40 \times 40$ grid.

Simulated distributions

Given the response surface fitted to the observed pattern of occurrence and the bioclimate values estimated for the AFE grid cells, the likelihood of occurrence for any given combination of values of the bioclimate variables may be assessed. Where necessary, the response surface is extrapolated in order to make such assessments. The same locally-weighted regression procedure and tricube weighting as for the fitting of the surface is employed when evaluating the probability of occurrence under given climate conditions. Any extrapolations thus are conservative and become asymptotic to the closest marginal fitted values.

The simplest test of any response surface is provided by its ability to simulate the observed species' distribution given the present bioclimate values for each AFE grid cell. We have performed such simulations for each of the eight species examined in the present study. Inevitably, because a degree of smoothing is inherent in the fitting of the response surface, a low probability of occurrence is simulated in many grid cells where the species is not observed to occur. It is therefore necessary to determine a threshold probability value for each species that 'best' represents the species observed pattern of occurrence (Table 1).

If the threshold is set high then most or all of the simulated occurrences will coincide with observed occurrences, although many of the observed occurrences will not be simulated. If, alternatively, the threshold is set low, then the majority or all of the observed occurrences will be simulated, although many of the simulated occurrences will not coincide with observed occurrences. The definition of the 'best' value for the threshold thus is not straightforward. It is necessary to optimize both criteria simultaneously; a majority of the observed occurrences should be simulated and the majority of the simulated occurrences should coincide with observed occurrences. We have calculated both criteria as proportions; the proportion of ob-

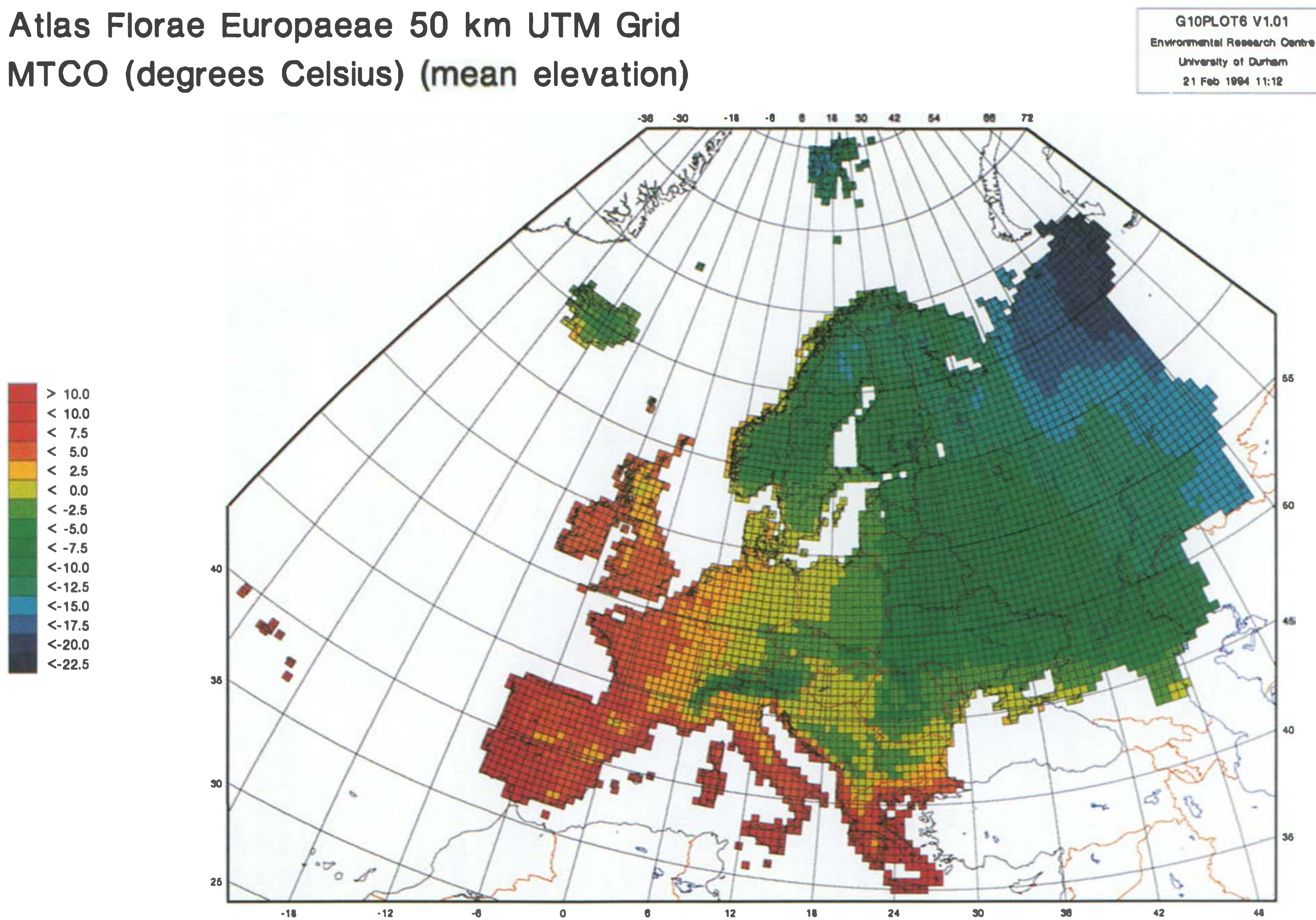

FIG. 2. Mean temperature of the coldest month (MTCO) (°C) interpolated for points located at the geographical centre and mean elevation of each AFE grid cell.

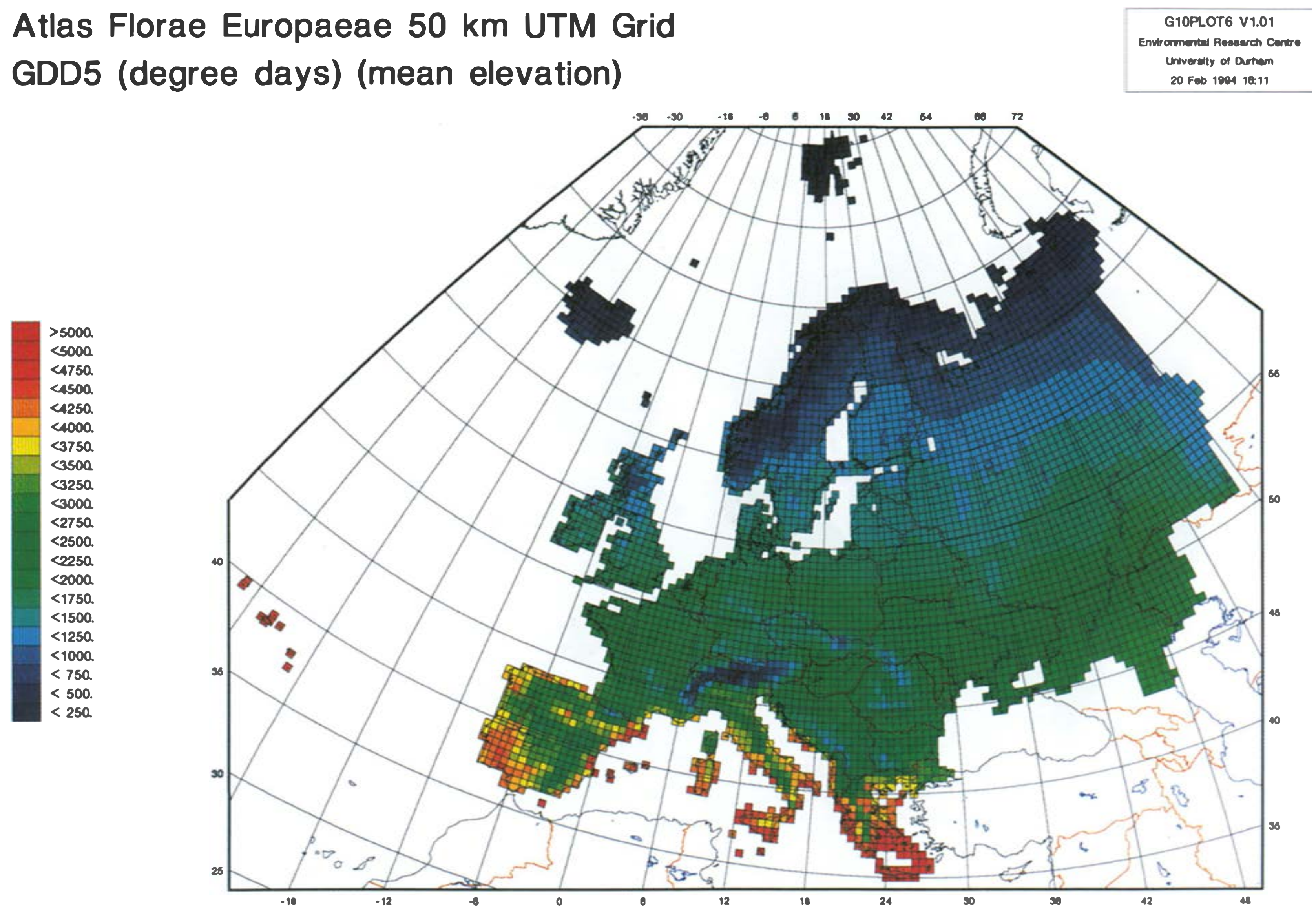

FIG. 3. Temperature sum above a threshold of 5°C (GDD5) (day degrees) interpolated for points located at the geographical centre and mean elevation of each AFE grid cell.

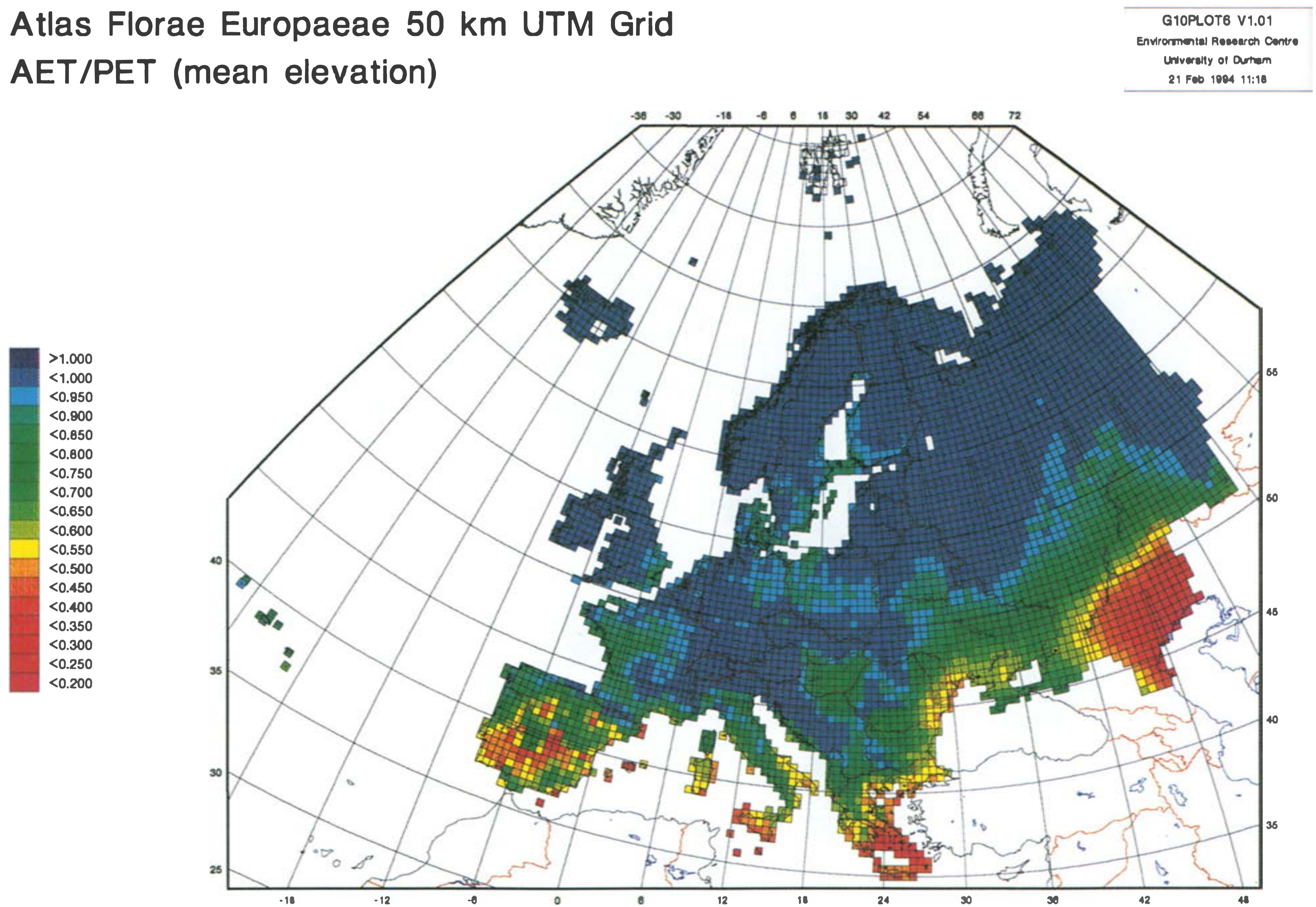

FIG. 4. Ratio of actual to potential evapotranspiration (AET/PET) estimated for points located at the geographical centre and mean elevation of each AFE grid cell.

TABLE 1. Numbers of occurrences observed and simulated.

		Present climate					OSU 2 × CO_2 scenario		UKMO 2 × CO_2 scenario	
Species	Recorded occurrences	Simulated occurrences	κ	P1*	P2†		Simulated occurrences	P2	Simulated occurrences	P2
Picea abies	1990	2042	0.844	0.927	0.904		1155	0.905	477	0.857
Tilia cordata	1619	1691	0.682	0.819	0.784		1490	0.493	960	0.290
Abies alba	436	462	0.623	0.681	0.643		783	0.163	544	0.068
Quercus ilex	405	466	0.708	0.793	0.689		1052	0.198	727	0.142
Hymenophyllum wilsonii	133	172	0.773	0.895	0.692		128	0.148	250	0.000
Erica vagans	103	123	0.655	0.728	0.610		313	0.048	223	0.004
Pulsatilla vulgaris	409	534	0.613	0.753	0.577		325	0.185	373	0.011
Silene acaulis	470	360	0.708	0.649	0.847		298	0.775	160	0.506

*P1 is the proportion of the recorded occurrences for which presence is simulated at or above the chosen probability threshold.
†P2 is the proportion of the simulated presences, at or above the chosen probability threshold, that coincide with recorded occurrences.

served occurrences simulated (*P*1) and the proportion of simulated occurrences coinciding with observed occurrences (*P*2). We also have calculated the kappa statistic (κ) (Monserud, 1990; Prentice *et al.*, 1992) for each simulation and have chosen that threshold (in increments of 0.05) that maximizes the value of this statistic. The use of individual grid cells to compute κ gives conservative values for this statistic; these values may be assessed using the subjective guidelines given by Monserud (1990). The values of κ, *P*1 and *P*2 at the chosen threshold are reported for each species (Table 1).

GCM scenarios

Having fitted a response surface for a species, and given that this may be used to simulate the species' probability of occurrence for any given combination of values of the three bioclimate variables to which the surface was fitted, it is now possible to explore the implications of forecast future climate changes with respect to the potential distribution of the species. We have examined four GCM simulations for radiative forcing equivalent to a doubling of pre-industrial concentrations of atmospheric carbon dioxide. Two of these simulations exhibit high sensitivity, Mitchell (1983) (UKMO) and Manabe & Wetherald (1987) (Geophysical Fluid Dynamics Laboratory—GFDL) whereas two exhibit relatively lower sensitivity, Schlesinger & Zhao (1989) (OSU) and Hansen *et al.* (1988) (Goddard Institute of Space Sciences—GISS). We present here the results for one from each group of simulations, UKMO and OSU. These two GCMs have spatial resolutions of 5° × 7.5° and 4° × 5° respectively.

No GCM currently delivers realistic climate scenarios at a scale compatible with those at which we observe patterns in terrestrial ecosystems. It conventionally is believed, however, that the magnitude of the relative changes between the control and 2 × CO_2 runs for any one GCM may be used to approximate the coarse-scale pattern of possible climate change. We have used the GCM scenarios in this way to create 'overlays' of the smoothed climate change signals. These then have been applied to the detailed patterns of interpolated 'present' climate in order to obtain the two 2 × CO_2 scenarios that we have used. The inherent inconsistency between spatial scales (M. Claußen & W. Cramer, unpublished manuscript) cannot be resolved satisfactorily until higher-resolution GCMs become available. Meanwhile, the procedure adopted here should be seen as a compromise that aims to generate climate scenarios with a scale appropriate for the investigation of the response of large-scale vegetation patterns.

The anomalies between the control and 2 × CO_2 runs were used for each GCM. Temperature anomalies were expressed as differences whereas precipitation anomalies were expressed as ratios. Smooth overlays of these anomalies were obtained by fitting thin-plate Laplacian spline surfaces (Hutchinson, 1989) with longitude and latitude as the independent variables and the anomaly as the dependent variable. Interpolation of the anomalies to the AFE grid cells then was performed using the spline surfaces. The mean monthly temperature and precipitation anomalies were interpolated for each AFE grid cell and then were used to modify the previous values interpolated from the meteorological station data. The modified values then were used to compute modified bioclimate scenarios corresponding to each GCM forecast.

Potential future distributions

The potential future distributions were generated using the same approach as for the simulated present distributions but substituting the GCM-derived bioclimate scenarios instead of the bioclimate values estimated from the observed meteorological data. The probability threshold determined for each species from the simulation of its present distribution was applied to the maps of its potential future distribution.

THE SPECIES AND THEIR RESPONSE SURFACES

Selection of the species*

Eight species were selected that represent different general

*We follow Tutin *et al.* (1964, 1968, 1972, 1976, 1980) for species nomenclature and taxonomy.

types of distribution within the British Isles and/or Europe. Four of the species selected are trees, three are broad-leaved herbs and one is a filmy fern. One of the trees and all of the non-tree species are native to the British Isles, although all five are relatively restricted in occurrence and are of conservation interest. Of the other three trees, two are relatively widely planted in the British Isles, one of them at least also having reached the area as a native species on a number of occasions prior to the last glacial maximum; the third is not commonly planted although it did reach the British Isles as a native during the last and earlier interglacials.

The four trees exhibit boreal, widespread continental, central European and Mediterranean patterns of distribution respectively, whereas the non-tree species exemplify Arctic-Alpine, oceanic west European, north European and Lusitanian distribution patterns.

Picea abies (L.) Karsten

Picea abies (Norway spruce) (Fig. 14A) occurs widely throughout northern mainland Europe where over large areas it is the dominant species in the boreal forests. It occurs also in the mountains of central and south-eastern Europe as a component of the montane forest belt. Ecologically, *P. abies* is a shade-tolerant, canopy-dominant late-successional species. It tends to be displaced by broad-leaved competitors on more fertile and/or more calcareous soils and is replaced by *Pinus sylvestris* (Scots Pine) on soils that are waterlogged, extremely nutrient poor/acid or extremely shallow. It has continued to expand its range westwards both in Fennoscandia and the Alpine region during the late Holocene (Huntley & Birks, 1983; Huntley & Webb, 1989). During previous interglacials, as well as during interstadials, *Picea abies* extended westwards as far as the British Isles (West, 1968, 1980; Huntley & Birks, 1983).

The response surface (Fig. 5) shows highest probabilities of occurrence in regions of cold winter conditions and relatively low temperature sum. The probability of occurrence declines rapidly at MTCO values of > -2°C. This mirrors the absence of the species from the more oceanic fringes of Scandinavia as well as from the mountains of western Europe. This is generally attributed to the frost sensitivity of seedlings and their failure to survive in regions that lack a consistent winter snow cover. The probability of occurrence also declines sharply at GDD5 values of below *c*. 600 day degrees and diminishes steadily as AET/PET is reduced.

Tilia cordata Miller

Tilia cordata (small-leaved lime) is widely distributed from the British Isles eastwards, displaying distinct northern, southern and western limits within the area being examined (Fig. 15A). Its eastern limit lies a little to the east of the edge of the study area (Pigott, 1991). Ecologically, it is a long-lived canopy-dominant component of mixed deciduous forests. Its seedlings are relatively shade-tolerant (Paice, 1974) and it is able to grow upon a wide range of soils (Paice, 1974), although not on those that are waterlogged or extremely acid. It reached a Holocene maximum in terms both of range limits and abundance around 5000 BP (Huntley & Birks, 1983). Subsequently, it has shown little reduction in range, although its relative abundance in the remaining deciduous forests is apparently much reduced, probably in part at least as a result of selective felling.

Experimental studies have shown that the failure to produce viable seeds at its northern limit in the British Isles is related to the temperature sensitivity of pollen germination and pollen-tube growth rate (Paice, 1974; Pigott & Huntley, 1981). In contrast, in the more continental climate of Finland fertilization is successful but the fertilized ovules fail to develop to maturity during the short summer at the species' northern limit (Pigott, 1981). In both cases a limitation by summer warmth is apparent; this is reflected by the response surface (Fig. 6) that shows few occurrences at GDD5 values of < 1000 day degrees. Those few cases where the response surface extends to lower values of GDD5 are associated with milder winters (MTCO > -9°C) and high moisture availability.

The response surface also shows an upper limit of GDD5 at *c*. 3000 day degrees and of MTCO at *c*. 6°C. This corresponds to the absence of *T. cordata* from all but mountainous areas of southern Europe. The lower limit of AET/PET at *c*. 0.6 similarly reflects the southern and especially south-eastern limits of the tree as the seasonally-dry regions around the Mediterranean and in the steppes are approached.

Abies alba Miller

Abies alba (silver fir) (Fig. 16A) principally is associated with the montane forests of central and southern Europe where it especially is characteristic of the Abieti-Fagetum in which it shares canopy dominance with *Fagus sylvatica* L. (Beech) (Ellenberg, 1988). It is a long-lived late-successional species with shade-tolerant seedlings and is tolerant of a wide range of soils other than those that are waterlogged. Although it exhibits a marked north-westward limit in mainland Europe at the present day, it was found in western Ireland during the Gortian interglacial (Jessen, Andersen & Farrington, 1959) and in parts of the British mainland during many previous interglacials (West, 1968, 1980).

The relatively limited geographical range of *A. alba* is reflected by the response surface (Fig. 7) that shows a limited range in climate space. A marked sensitivity to winter temperatures is shown with no occurrences at MTCO values < -10°C. An interaction between MTCO and GDD5 is also apparent with occurrences at higher MTCO values only at higher GDD5 values. The frequency of occurrence declines rapidly at lower values of AET/PET and in this respect parallels the behaviour of the two previous species.

Quercus ilex L.

Quercus ilex (holm oak) is associated primarily with the

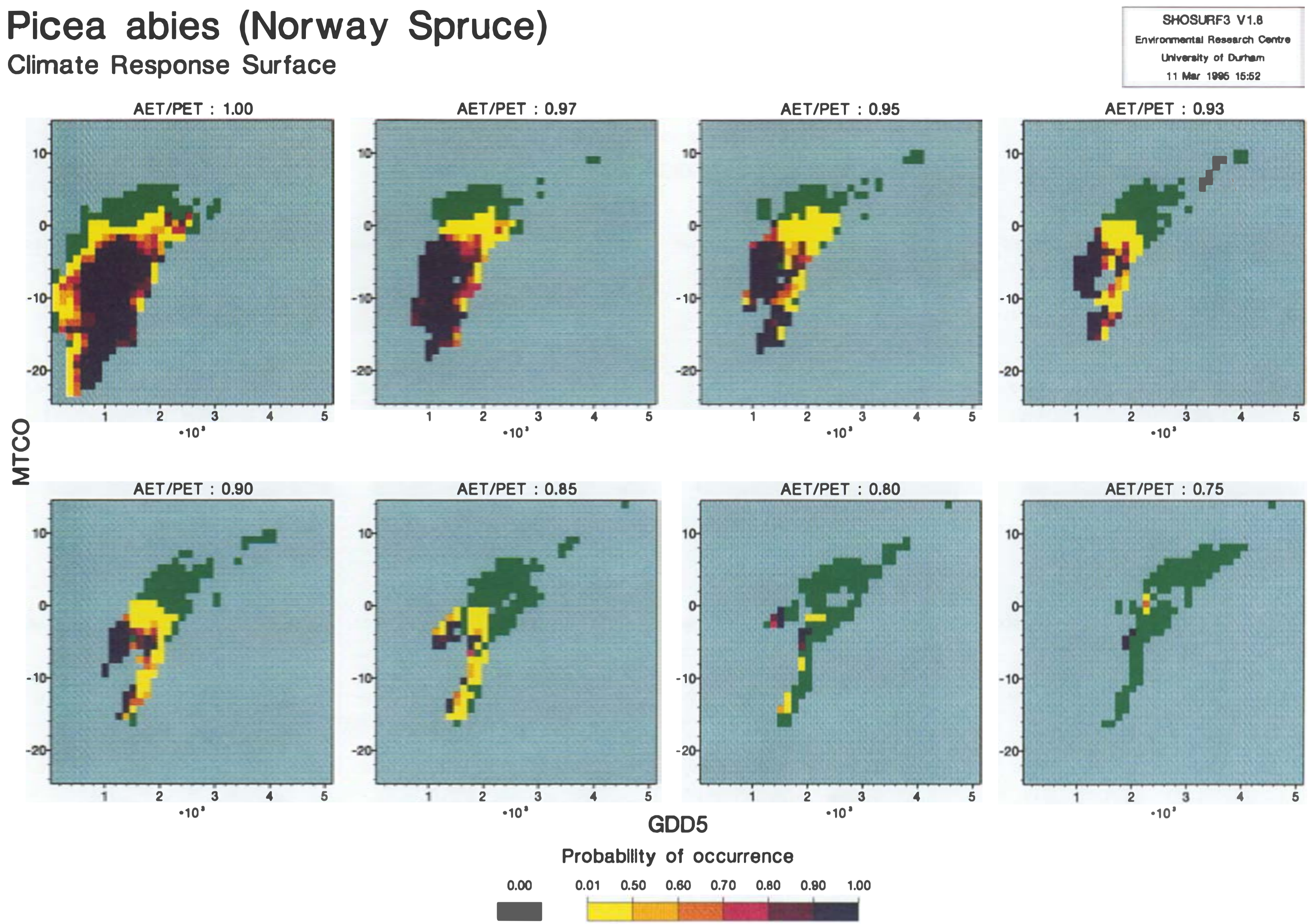

FIG. 5. *Picea abies* response surface. Three-dimensional climate response surface; each panel represents a cross-section at a different value of AET/PET (ratio of actual to potential evapotranspiration). The x-axis represents the annual temperature sum above a threshold of 5°C (in units of thousands of degree-days) and the y-axis represents the mean temperature of the coldest month (°C). The dark green shaded area represents combinations of climate conditions that are found within Europe but under which the probability of occurrence of the species is zero; the yellow shading represents areas of climate space where the probability of occurrence of the species is below the threshold determined using the kappa statistic (see text). The remaining shades indicate increasing probabilities of occurrence.

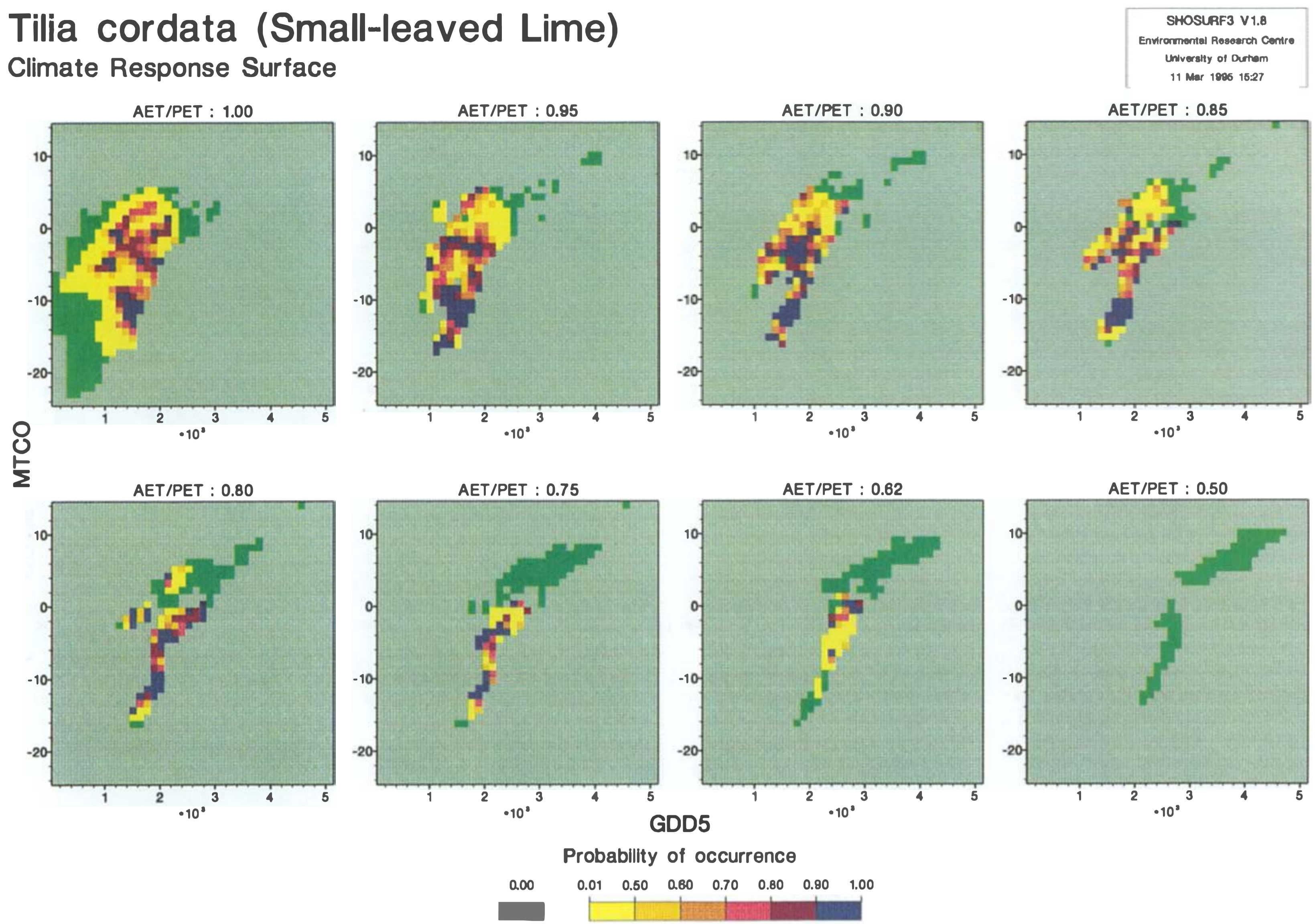

FIG. 6. *Tilia cordata* response surface. (See caption to Fig. 5.)

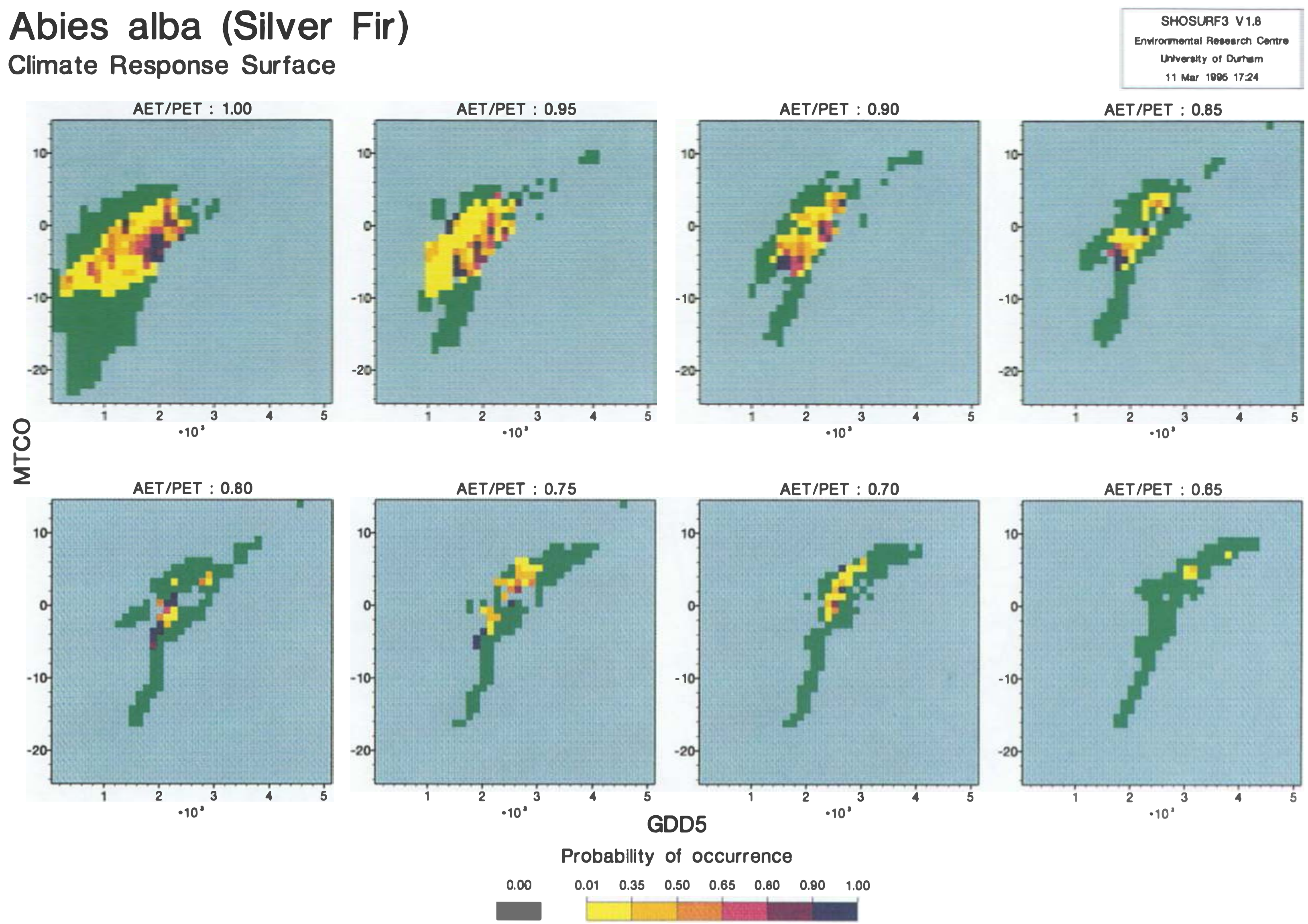

FIG. 7. *Abies alba* response surface. (See caption to Fig. 5.)

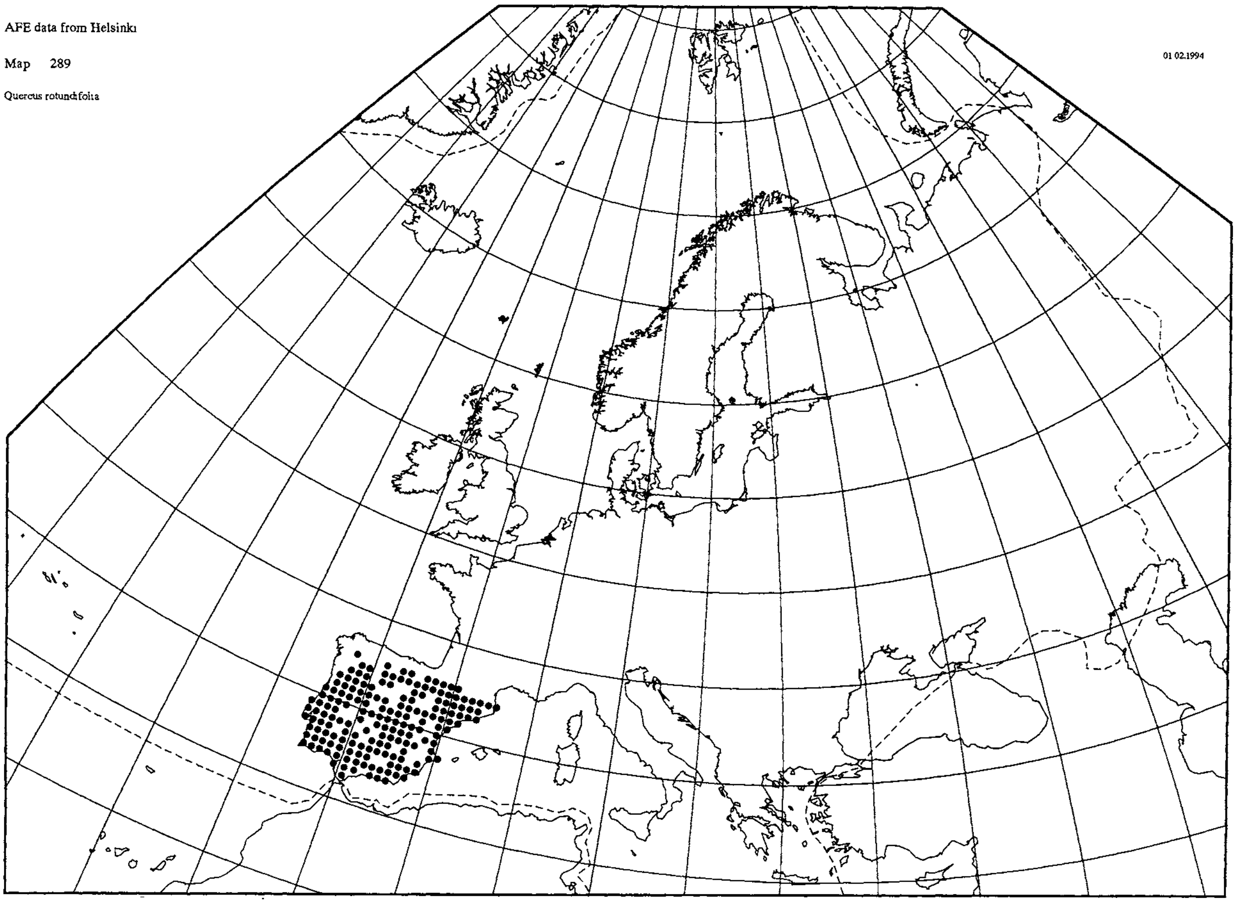

FIG. 8. *Quercus rotundifolia* distribution: observed distribution (Jalas & Suominen, 1976).

evergreen forests of sclerophylls that characterize the Mediterranean region. Exceptionally it may ascend as high as 1000 m above sea level, as in parts of southern Italy (Barbero, Loisel & Quézel, 1992), although it is distributed principally in lowland areas of southern Europe (Fig. 17A). It is widespread around the Mediterranean with the exception of much of the Iberian Peninsula where it is replaced by the closely related *Q. rotundifolia* Lam. (Fig. 8). It is shade-tolerant and is able to dominate the canopy on both calcareous and non-calcareous soils (Jones, 1959). During the Holocene it expanded northwards up the western seaboard of mainland Europe (Huntley & Birks, 1983), although it is doubtful that it reached the British Isles as a native. Its present occurrences in Britain are the result of introduction and it has been widely planted as an ornamental; it has become locally naturalized at a small number of localities in southern England (PMB, unpublished observations).

The response surface (Fig. 9) shows a sharp limit in relation to MTCO at a value of -3°C; this is markedly lower than the threshold value of 5°C for warm-temperate evergreens used by Prentice *et al.* (1992) but corresponds to the ability of *Q. ilex* to survive absolute minimum temperatures of -10°C to as low as -24°C (Boudy, 1948–55). Although the response surface shows some occurrences at GDD5 values of <2000 day degrees, the optimum of the surface lies at values in the range 2500–4500 day degrees. The greater drought-tolerance of this species compared to the three foregoing species is reflected by the extension of the range to AET/PET values <0.4; this corresponds to the observed ability of the species to grow in areas of North Africa with as little as 300 mm annual precipitation.

Hymenophyllum wilsonii Hooker

Hymenophyllum wilsonii (Wilson's filmy fern) is a small pteridophyte, similar in size to many of the large oceanic bryophytes amongst which it typically grows. Like those of these non-vascular cryptogams, *H. wilsonii* leaves are only one cell thick and lack a cuticle. The plant consequently is extremely sensitive both to dry conditions and to high light intensities. *H. wilsonii* is, as a result, limited to the most oceanic parts of north-west Europe (Fig. 18A) where it typically occurs as a component of the cryptogam-dominated ground flora of deciduous woodlands. Edaphically it is tolerant neither of calcareous nor of waterlogged or peaty soils.

The response surface (Fig. 10) reflects the species' intolerance of even slight drying, with almost no occurrences at

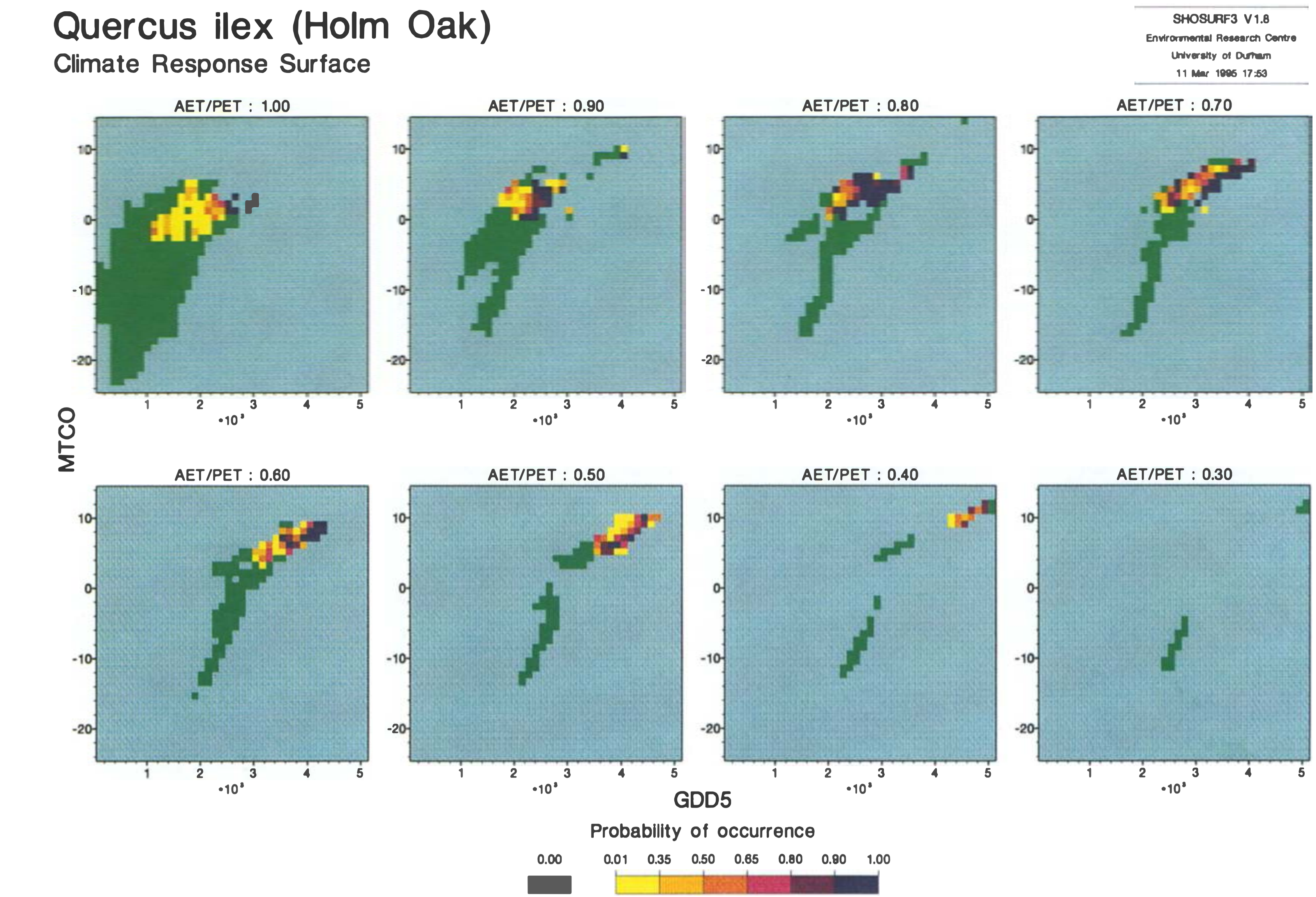

FIG. 9. *Quercus ilex* response surface. (See caption

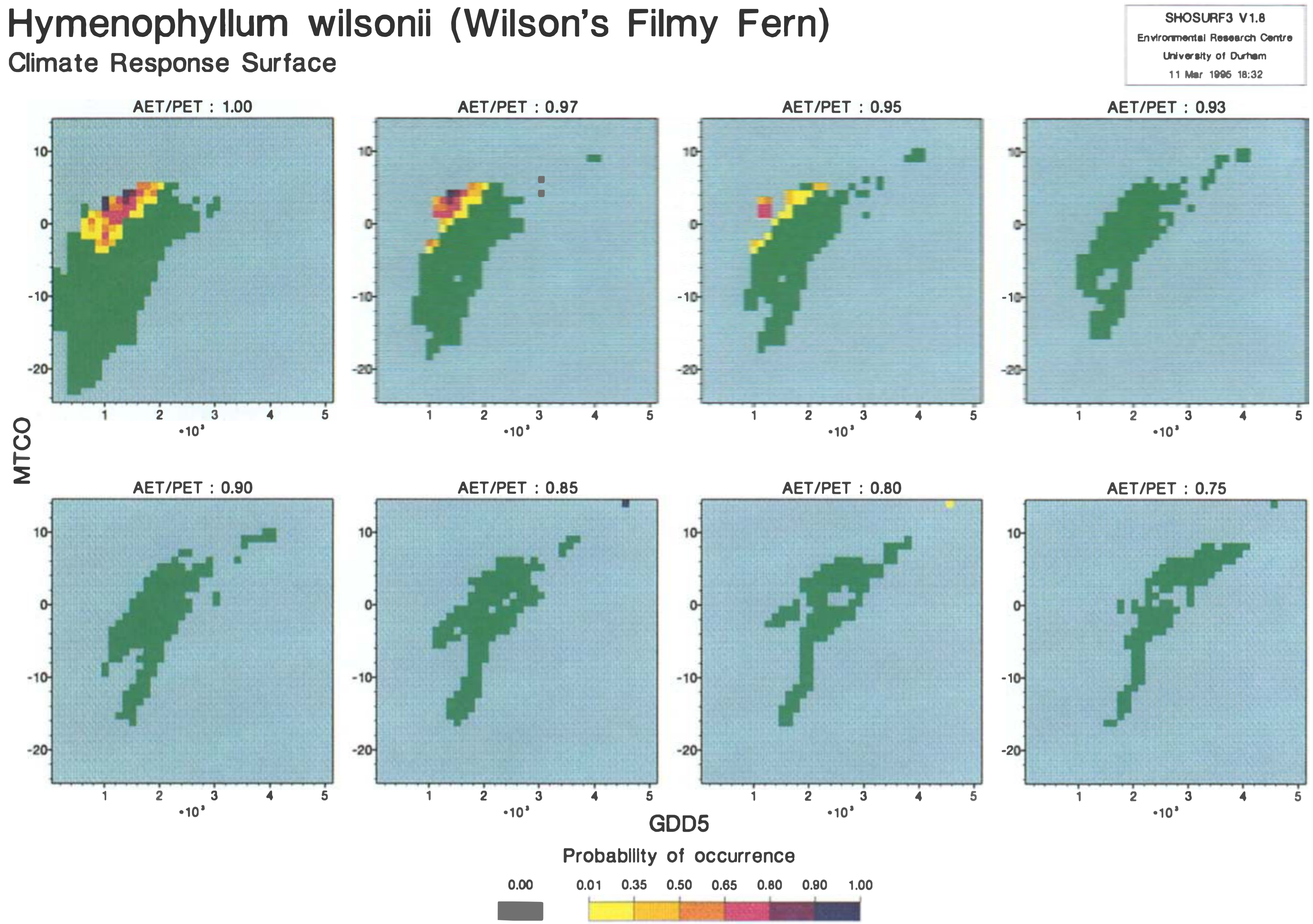

FIG. 10. *Hymenophyllum wilsonii* response surface. (See caption to Fig. 5.)

AET/PET values < 0.95. It also shows the species to be limited by values of MTCO $< -4°C$ and generally to occur within a limited range of values of GDD5 between *c.* 600 and *c.* 2400 day degrees. The exceptional occurrences are in the Azores and may reflect either poor estimation of the climate of these isolated Atlantic islands or limitation of the species to high elevations on these mountainous islands.

Erica vagans L.

We were unable to locate a map of the overall European range of *Erica vagans* (Cornish heath). Our map (Fig. 19A) hence has been compiled from a number of published sources of regional distributional data (Perring & Walters, 1982; Aseginolaza, 1984; Fraga, 1984; Dupont, 1990) from which data were transferred manually to the AFE grid; P. Montserrat (pers. comm.) also provided valuable information for Spain which was used to complete our map. The species proves to have a limited distribution, being found principally in western France and northern Spain with outlying localities in south-west England and north-west Ireland. Although its ecological limitations in south-west England have been the subject of considerable study (Coombe & Frost, 1956; Frost, 1968; Hopkins, 1983) less is known about its ecology in the central parts of its range. It is apparent, however, that whereas it is limited to areas of serpentine and gabbro in south-west England, elsewhere it tolerates soils derived from a much wider range of bedrocks and exhibiting a considerable range of base-status and drainage (Dupont, 1975, 1990). In stature it is a dwarf shrub, rarely exceeding 50 cm; it is found principally as a component of open heathlands from the maritime to sub-alpine zones and rarely in shaded situations.

The limited area of occurrence depicted by the response surface (Fig. 11) reflects the limited geographical range of *E. vagans*. The species range exhibits marked limits at low values of MTCO and GDD5 with no occurrences at values of $< 1°C$ or $< c.$ 2000 day degrees respectively. Only a moderate degree of drought is tolerated, with no occurrences at AET/PET values < 0.65.

Pulsatilla vulgaris Miller

Pulsatilla vulgaris (Pasque flower) has a distribution that is centred in the lowland regions of northern mainland Europe (Fig. 20A). Although in some regions it exhibits restriction to calcareous soils, thus behaving as an apparent calcicole, elsewhere it is tolerant of soils of much lower pH (Wells & Barling, 1971). It is a low-growing, shade-intolerant, long-lived herb typically found in grassland communities; whereas it is restricted to relatively low elevations near its north-western limit, it ascends to 630 m in Bavaria (Wells & Barling, 1971). It has suffered a marked reduction of its range in Britain during the second half of the twentieth century (Perring & Walters, 1976, p. 19) (Fig. 20A); this has been attributed primarily to changes in land use with arable agriculture extending into areas of semi-natural grasslands formerly used as grazing land. It is unclear whether the sparse occurrences in southern parts of the former USSR reflect a naturally sparse distribution, under-recording or a genuinely but unnaturally sparse distribution as a result of anthropogenic activities removing most areas of suitable habitat; calcareous substrates are, however, infrequent in this region.

The response surface (Fig. 12) indicates a limitation to areas with GDD5 $> c.$ 1000 day degrees and MTCO $< 7°C$. Conversely, the species is also absent where GDD5 exceeds *c.* 3000 day degrees or MTCO is $< -9°C$. Perhaps surprisingly, the response surface indicates a rapid decline in occurrences at AET/PET values < 0.8 and absence at values < 0.7. This corresponds, however, to experimental evidence indicating that the seedlings are susceptible to desiccation (Wells & Barling, 1971).

Silene acaulis (L.) Jacq.

Silene acaulis (moss campion) is an Arctic-Alpine species, exhibiting the geographical distribution typical of this phytogeographic element (Fig. 21A). It is a cushion-forming herb capable of living for considerable periods under harsh conditions if free from shade and/or competition. Although it frequently exhibits a degree of calcicoly, in some regions it occurs on soils derived from acid rocks such as granite (Jones & Richards, 1962). Within the alpine dwarf-herb communities where it occurs it exhibits considerable ecological amplitude, being found across a range of habitats from those with perpetually irrigated soils and extended duration of snow-lie (McVean & Ratcliffe, 1962) to those of exposed summits and ridges where snow accumulation is minimal and desiccation may occur in any season (Jones & Richards, 1962).

The response surface (Fig. 13) shows that the distribution of *S. acaulis* in climatic space is strongly concentrated in those regions where GDD5 values are $< c.$ 1500 day degrees and MTCO values are $< 5°C$. The species also shows a marked reduction in frequency of occurrence when AET/PET values are < 0.95. The extension of the species to regions with GDD5 values approaching zero and MTCO values $< -22°C$ corresponds to the evidence of its ability to produce viable seed in the high Arctic (Jones & Richards, 1962) and to survive exposure to temperatures as low as $-196°C$ given previous cold acclimation (Larcher, 1980). Its general limitation to relatively high values of AET/PET corresponds to its observed limitation to moist habitats at its more southerly localities in Britain (Jones & Richards, 1962).

The response surfaces, being based upon the recorded distribution of the species, represent only their realised climatic niches and not their overall climatic potential. Given the observed sensitivity of the present species in particular to shade and/or competition, the possibility arises that its climatic potential may considerably exceed its realized climatic niche. Furthermore, the observed climatic limits of the species may, in fact, be the limits of its competitors rather than its own limits. However, this only would invalidate the use of the response surface to predict potential future distribution if it were likely that conditions of competition also would be changed in the future. This seems unlikely, given the potential for rapid spread by

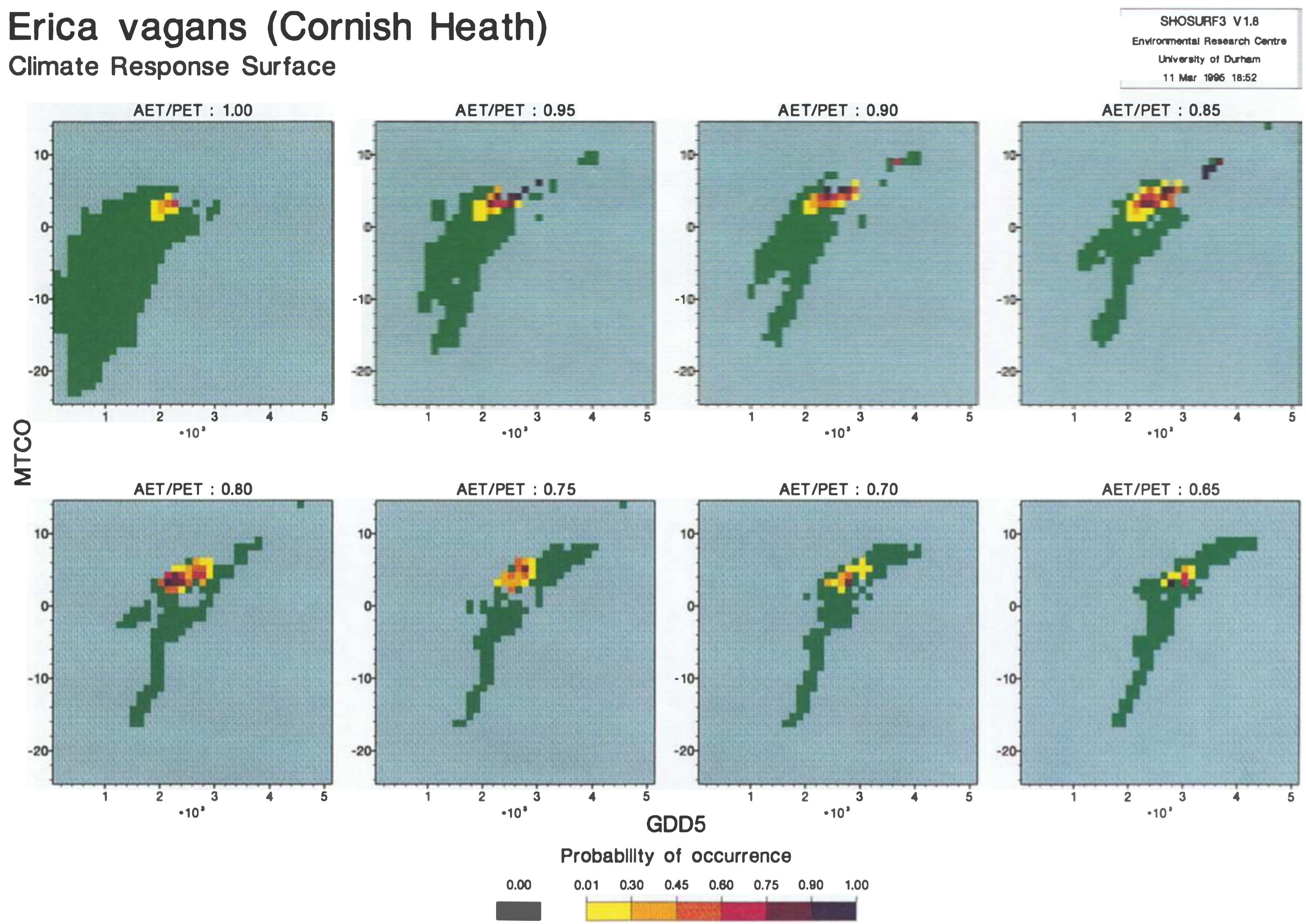

FIG. 11. *Erica vagans* response surface. (See caption to Fig. 5.)

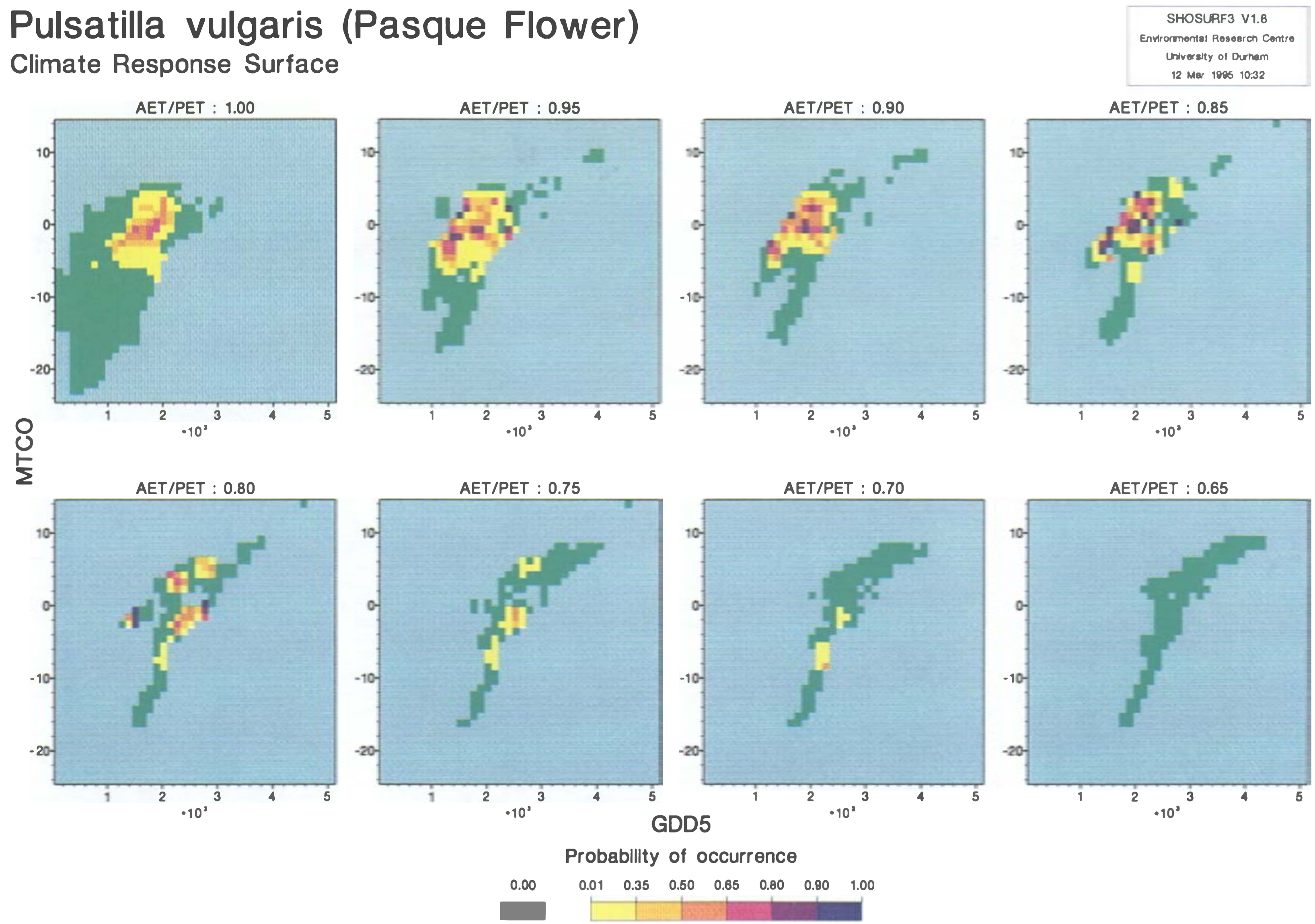

FIG. 12. *Pulsatilla vulgaris* response surface. (See caption to Fig. 5.)

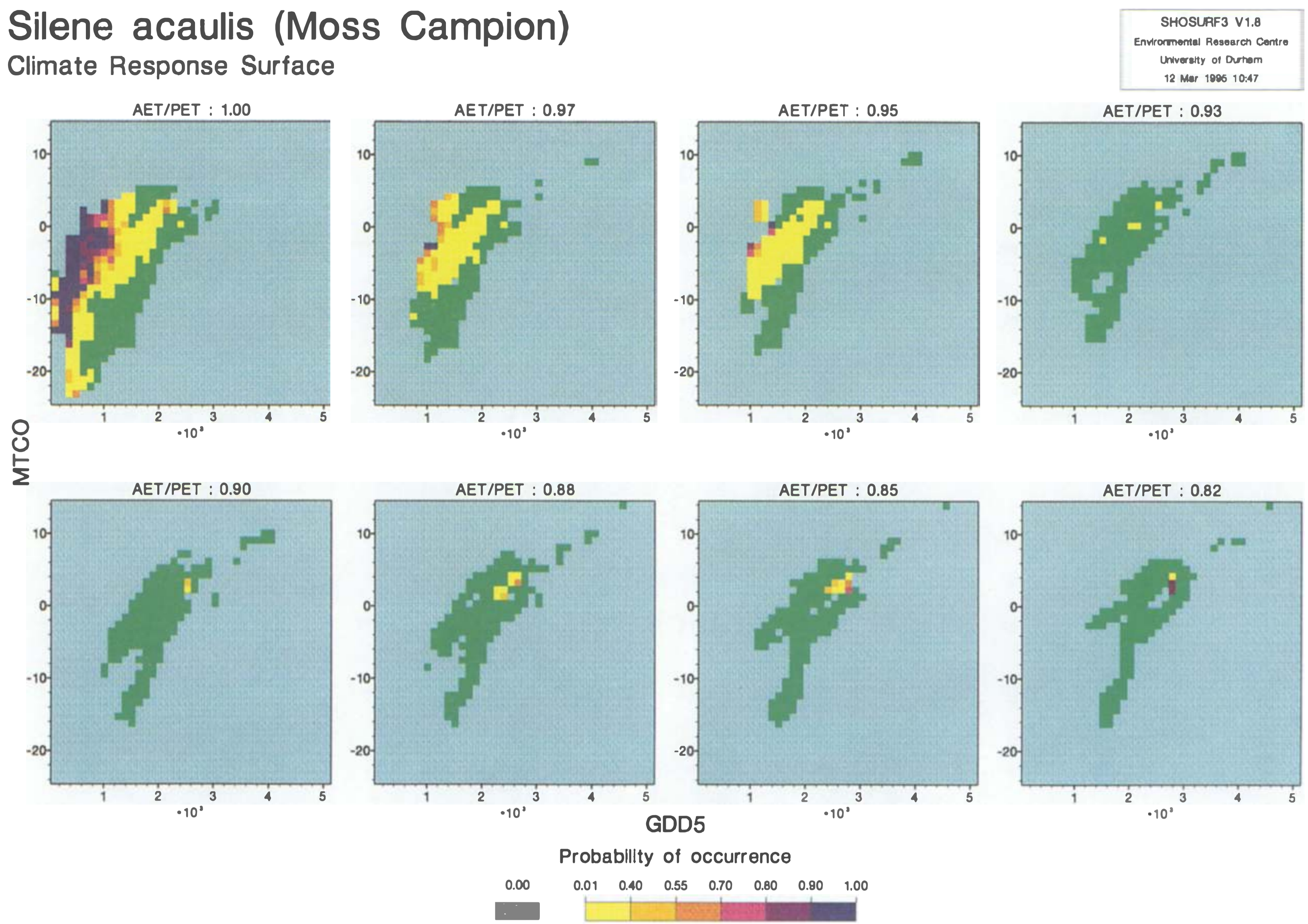

FIG. 13. *Silene acaulis* response surface. (See caption to Fig. 5.)

many of the tall, competitive herbaceous species capable of excluding *S. acaulis*.

SIMULATED PRESENT AND POTENTIAL FUTURE DISTRIBUTIONS

Picea abies

Using a threshold probability of 0.50 the simulated present distribution of *Picea abies* (Fig. 14B) corresponds closely to its observed distribution (Fig. 14A). Unlike the climatic limits modelled by Hintikka (1963) using mean temperatures of the coldest and warmest months, the response surface does not lead to simulated occurrences in the Pyrenees. This may relate to the use of GDD5 for the latter; this parameter, although closely correlated both to mean July temperature and to mean temperature of the warmest month, does not closely match these parameters in more western regions of Europe where the extended 'growing season' can offset the relatively cool summer temperatures that result from the moderating influence of the ocean.

The simulation for the OSU $2 \times CO_2$ climatic scenario (Fig. 14C) shows a marked north-eastward displacement of the range of *P. abies* and very limited occurrence around the central European mountains. The Arctic Ocean limits the potential for northward expansion with the result that the overall area occupied is much reduced. The simulation for the UKMO $2 \times CO_2$ climatic scenario (Fig. 14D) shows an even more severe reduction in overall range with the species now absent from most of Scandinavia as well as even more markedly reduced in central Europe.

Tilia cordata

The overall range of *Tilia cordata* is well simulated at a threshold probability of 0.50 (Fig. 15B); the principal area of discrepancy is with respect to the scattered occurrences recorded in northern Russia (Fig. 15A). When the distribution is simulated for the OSU $2 \times CO_2$ climatic scenario (Fig. 15C) a marked north-eastward displacement is again apparent. However, a displacement into the more mountainous regions of central Europe is also seen to some extent. Strikingly, the range in the British Isles does not overlap with either the observed range (Fig. 15A) or with that simulated for the present climate (Fig. 15B). The UKMO $2 \times CO_2$ climatic scenario (Fig. 15D) leads to no simulated occurrences in the British Isles and to a simulated distribution in central Europe and Scandinavia that mostly is restricted to higher elevations. Already in the OSU scenario simulation the range of *T. cordata* reaches northern Scandinavia and the Kola Peninsula; in the UKMO scenario simulation the species reaches the coast of the Arctic Ocean in northern Russia.

Abies alba

At a threshold probability value of 0.35 the present range of *Abies alba* is reasonably well matched by the simulation (Fig. 16B). The principal discrepancies relate to the sparse simulated occurrences at the western and southern margins of the range and the simulation of many occurrences in north-east Poland as well as scattered occurrences in Scandinavia, in both of which regions the tree is absent. These discrepancies are more marked than those for the two previous species and may indicate that for one of several possible reasons the range of *A. alba* cannot be so well modelled using the present approach. Amongst the possibilities we must include are: (1) the species' range is not in equilibrium with the present climate; (2) the climate of the mean elevation of those 50 km squares where the species occurs is not representative of the climate where the species grows; and (3) the species' range is determined by some other aspect of the climate apart from the three variables used in the present study.

A disequilibrium between the species' range and the present climate might arise either if the species' was limited also by some other aspect of the environment that varied on a regional scale or by interaction with some other organism that is sensitive to some other aspect of the environment, or else if the species had been unable to regain equilibrium with some relatively recent climatic change. The combination of longevity and the selective exploitation of *A. alba*, coupled to extensive deforestation of the area where occurrence is simulated in north-east Poland, provides support for the latter hypothesis. The absence of the tree from climatically apparently suitable areas of Scandinavia most probably reflects an inability to cross the dispersal barrier of the north-European lowlands at any time during the Holocene.

The occurrence of *A. alba* principally in montane forests may render the climate of the mean elevation a poor estimate of the climate in which it grows. However, this is not likely to be as important for such a mid-elevation species as it would be for species restricted either to the alpine zone or else to valley-bottom localities. Nonetheless, this may account for the sparse simulated occurrences in mountain areas near the species' range limits. The possibility that the species' range in part may be restricted by some other aspect of the climate cannot be excluded; however, no obvious candidate variable can be advanced.

The OSU $2 \times CO_2$ climatic scenario leads to a simulated range that is shifted markedly north-eastwards (Fig. 16C). This trend is even more marked in the simulation for the UKMO $2 \times CO_2$ climatic scenario (Fig. 16D) which shows the species principally occurring in northern Fennoscandia and north-west Russia with only scattered occurrences remaining in central Europe.

Quercus ilex

At a threshold probability of 0.35 the range of *Quercus ilex* is well simulated overall (Fig. 17B). The principal exceptions are the failure to simulate those parts of the recorded distribution where the species has been introduced, as for example in Britain, and the simulation of a more extensive range in the Iberian Peninsula where, as mentioned above, this species is replaced by a closely related endemic species (*Q. rotundifolia*, Fig. 8). These failures indicate that, on the one hand, the present climate of those areas to which the species has been introduced is neither consistent nor

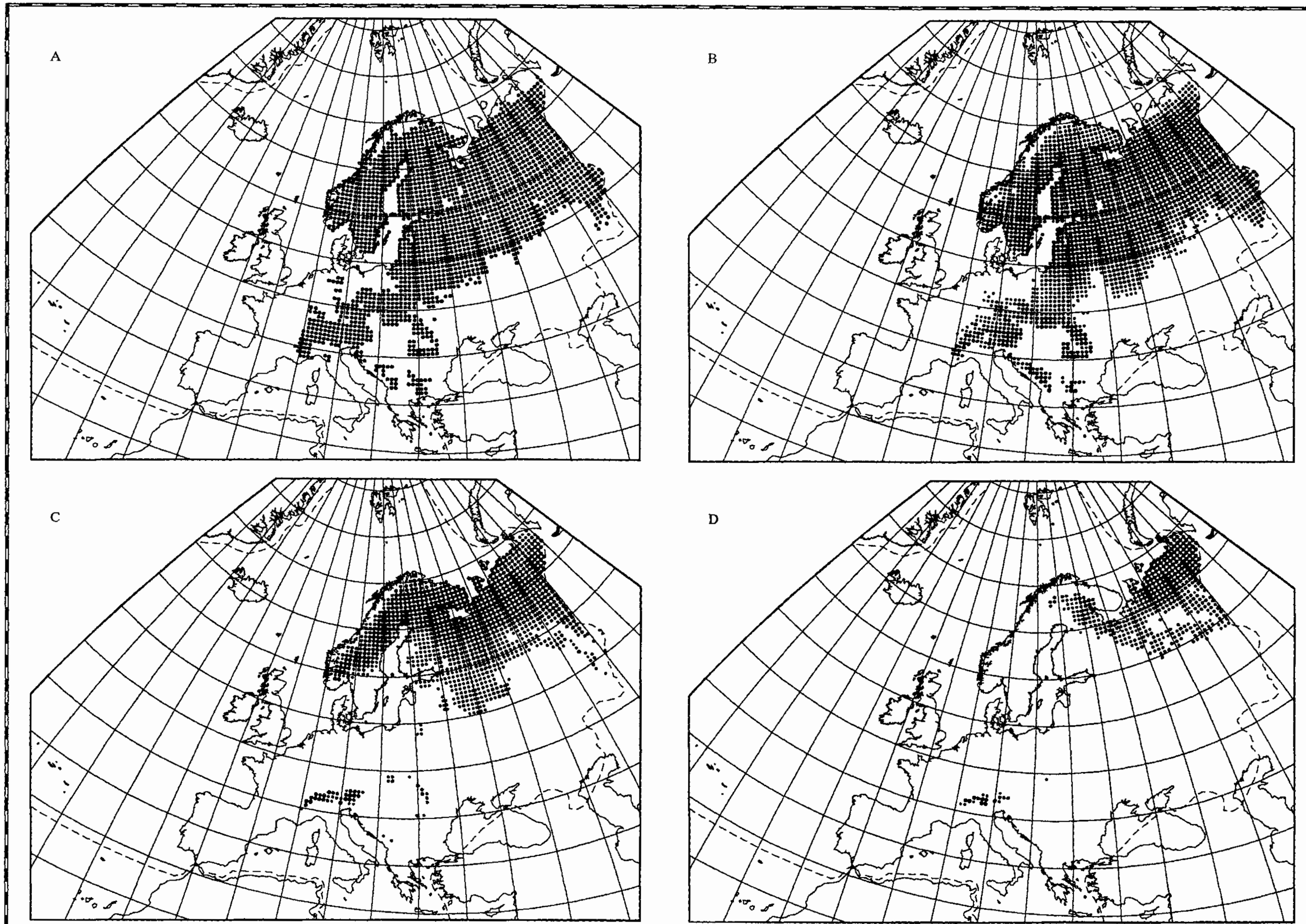

FIG. 14. *Picea abies* distributions: (a) Observed distribution (Jalas & Suominen, 1973); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.844$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.50; 90% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 93% of the observed occurrences being simulated.)

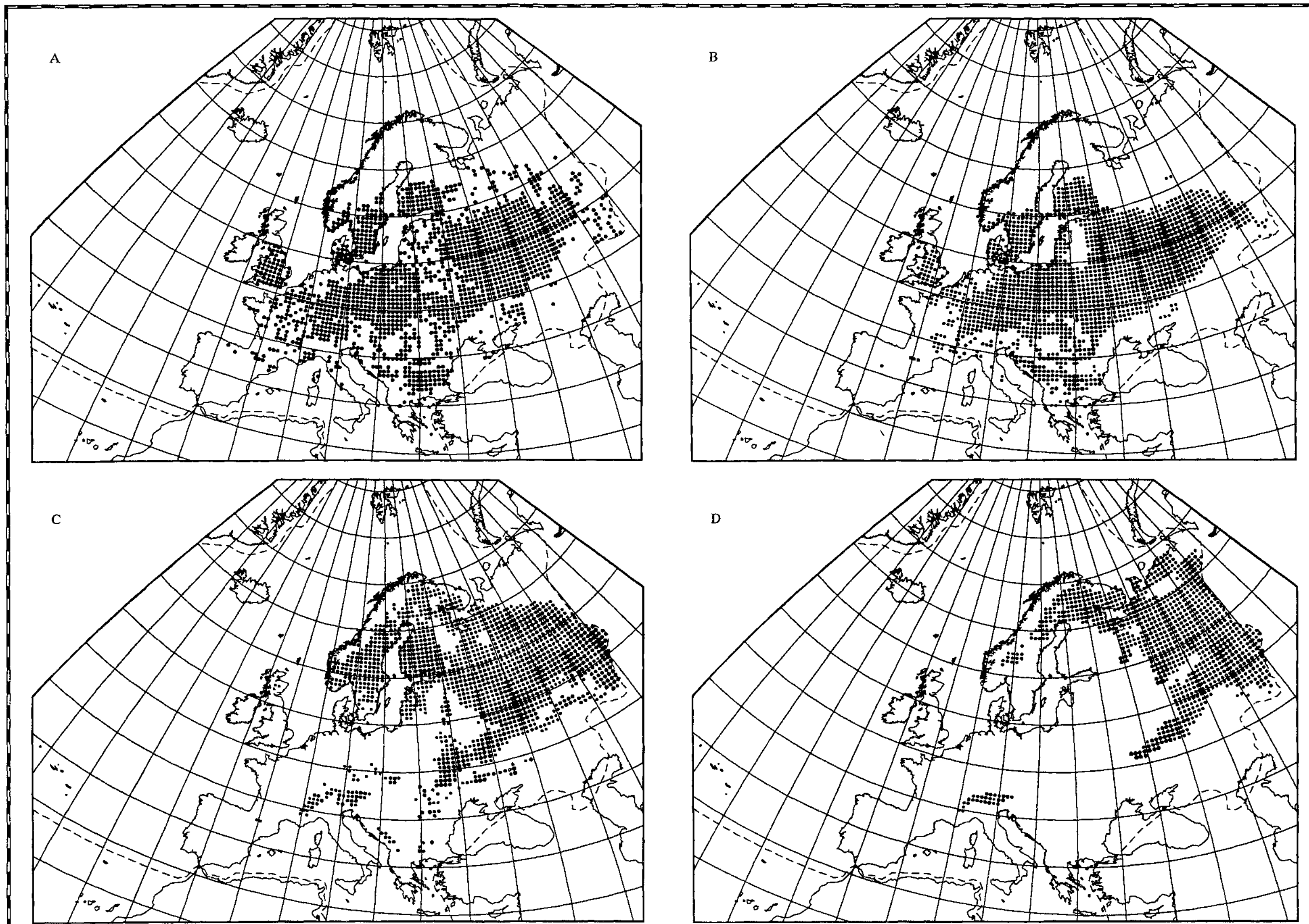

FIG. 15. *Tilia cordata* distributions. (a) Observed distribution (Pigott, 1991); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.682$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.50; 78% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 82% of the observed occurrences being simulated.)

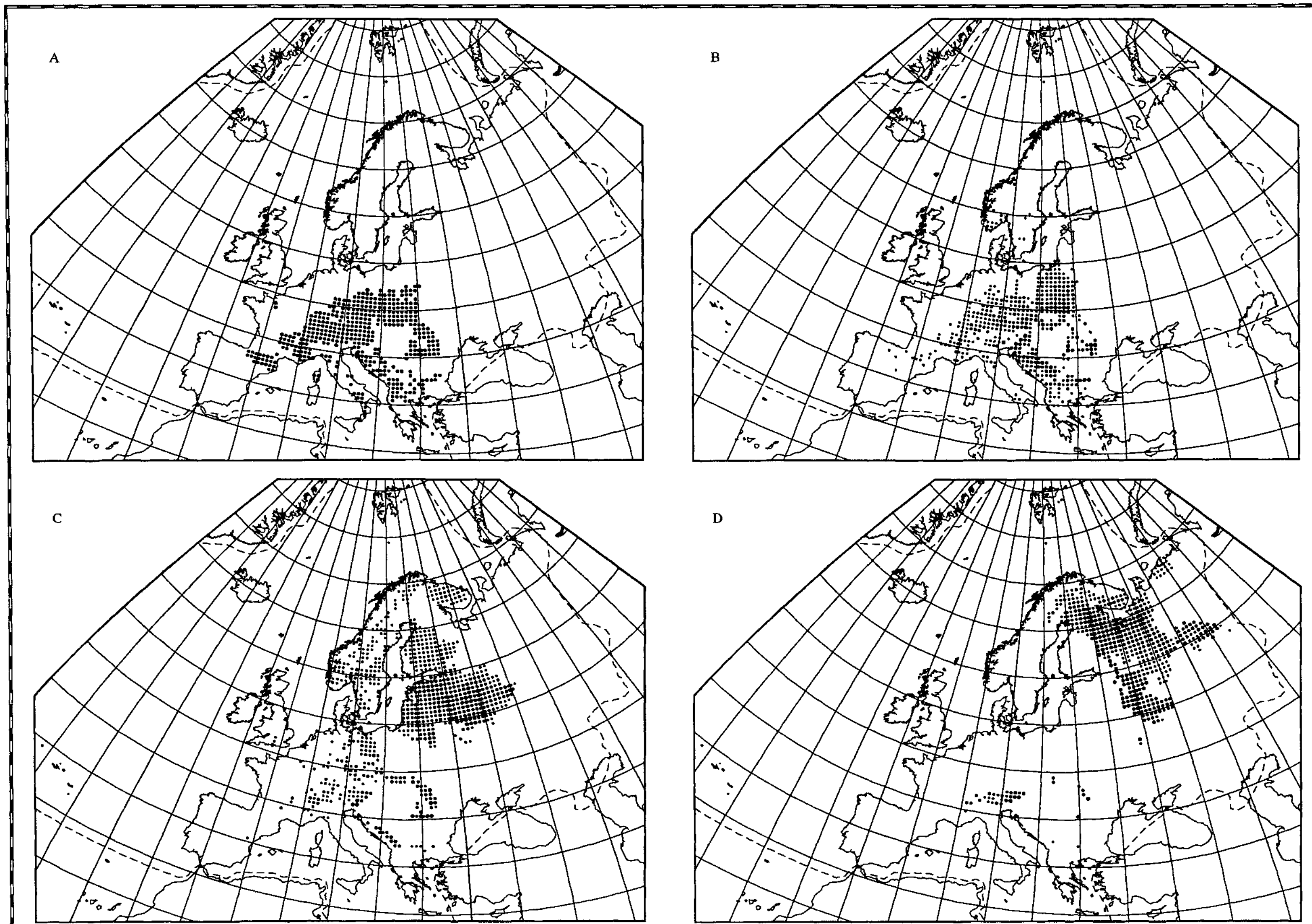

FIG. 16. *Abies alba* distributions. (a) Observed distribution (Jalas & Suominen, 1973); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.623$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.35; 64% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 68% of the observed occurrences being simulated.)

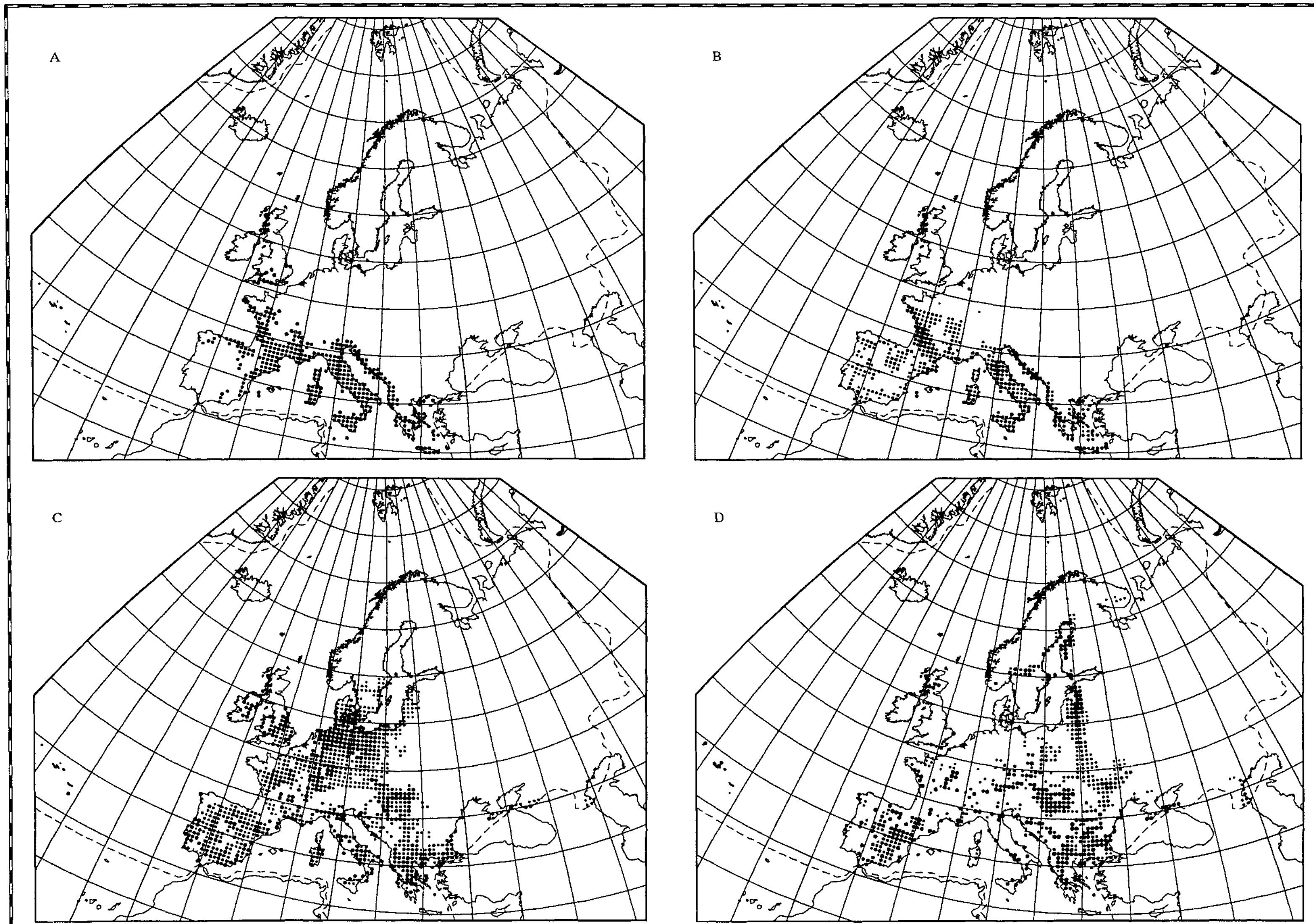

FIG. 17. *Quercus ilex* distributions. (a) Observed distribution (Jalas & Suominen, 1976); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.708$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.35; 69% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 79% of the observed occurrences being simulated.)

favourable and, on the other, that the species' absence from much of the Iberian Peninsula may be determined by competition with its congener rather than by a climatic limit. In this context it is perhaps noteworthy that Tutin *et al.* (1993) have reduced *Q. rotundifolia* to the rank of a subspecies of *Q. ilex*.

The OSU $2 \times CO_2$ climatic scenario leads to a simulated range that extends northwards into the British Isles and eastwards across the north European lowlands as far as southern Sweden and Poland reaching an extreme limit in Estonia (Fig. 17C). Unlike the three previous species, however, *Q. ilex* does not show any marked north-eastward displacement of its south-western range limit. This is entirely reasonable, given the species' present occurrence throughout much of North Africa, and corresponds to the simulation using the BIOME model of an extensive area of the 'Broadleaved evergreen forest' biome in south-western Europe for the same scenario (Cramer *et al.*, 1992).

The UKMO $2 \times CO_2$ climatic scenario leads to a more extreme result with the northern and eastern limits displaced even further (Fig. 17D) and the species absent from most of lowland northern Europe. The marked eastern limit reflects the north-south orientation of winter isotherms in eastern Europe and the strong winter temperature limit exhibited by this species.

Hymenophyllum wilsonii

The recorded distribution of *Hymenophyllum wilsonii* (Fig. 18A) is well matched by the simulation (Fig. 18B) at a threshold probability of 0.35. The principal discrepancy is a tendency for the simulated eastern limit in the British Isles to lie too far east. The simulated range for the OSU $2 \times CO_2$ climatic scenario (Fig. 18C) exhibits marked northward displacement, with occurrences simulated in Iceland and northern Norway. The southern limit in the British Isles and northern Europe shows a corresponding northward shift, whilst the species is no longer simulated in the Azores although it is now simulated in the far north of the Iberian Peninsula. This gap in the simulated distribution may be an artefact of the gap in the response surface (Fig. 10) that is in turn a consequence of the climatic gap between mainland Europe and the Azores. Alternatively, as noted above, it may result from a deficiency in the response surface resulting from the extreme relief of the Azores.

The range simulated for the UKMO $2 \times CO_2$ climatic scenario exhibits both a greater northward displacement and a shift from the coastal fringe of Scandinavia into the mountains of the interior. No occurrences are simulated in the British Isles for this scenario.

Erica vagans

With the minor exceptions of the failure to simulate the outlying occurrences recorded from the British Isles (Fig. 19A) and the simulation of scattered occurrences in Italy and Corsica where the species does not occur, the observed distribution of *Erica vagans* is well matched by the simulation at a threshold probability of 0.30 (Fig. 19B). The OSU $2 \times CO_2$ climatic scenario leads to a simulated range expansion, principally as a result of the north-eastern range margin shifting north-eastwards much more than the south-western range margin (Fig. 19C). This scenario leads to the simulation of an extensive range in the British Isles along with north-eastward expansion as far as northern Denmark and south-eastern Sweden.

In contrast, the UKMO $2 \times CO_2$ climatic scenario leads to a simulation with a much more marked shift of both the north-eastern and south-western range margins and, as a result, only a modest overall expansion, as opposed to a large shift, of range (Fig. 19D). There is very little overlap between the simulated range and the species' present distribution.

Pulsatilla vulgaris

At a threshold probability of 0.35 the simulated distribution of *Pulsatilla vulgaris* (Fig. 20B) well matches the recorded distribution (Fig. 20A). The principal area of discrepancy relates to the failure to simulate the scattered occurrences in the southern USSR, the alternative origins of which were discussed above. Whatever their origin, the failure to simulate these occurrences indicates that they are sparse in climatic as well as in geographical space.

The distribution simulated for the OSU $2 \times CO_2$ climatic scenario (Fig. 20C) is both reduced and markedly displaced compared to that simulated for the present climate (Fig. 20B). In central Europe the displacement is upwards into the more mountainous regions whereas in Scandinavia the displacement is relatively modest and occurs principally as a northward shift around the Baltic. The major loss of range is across the north European lowlands whereas the principal area of gain is across southern Russia.

The more extreme UKMO $2 \times CO_2$ climatic scenario leads to a simulated range (Fig. 20D) that hardly overlaps at all with the present distribution, being strongly displaced eastwards and having its centre in Russia. The only occurrences simulated in western Europe are in the highest elevation grid squares in the Alpine region.

Silene acaulis

The observed distribution of *Silene acaulis* (Fig. 21A) is well matched overall by the simulated distribution (Fig. 21B) using a probability threshold of 0.40. The most striking discrepancies relate to the areas of occurrence in northern Spain and the Pyrenees, the Carpathians and the Apennines, in all of which fewer occurrences are simulated than are observed. The same is seen around the Alps; in all cases this almost certainly relates to the use of climate values estimated for the mean elevation of the 50 km grid squares whereas in these regions *S. acaulis* is restricted to the upper elevations, occurring only above the treeline.

The OSU $2 \times CO_2$ climatic scenario leads to a simulated range (Fig. 21C) that is, at first glance, very similar to that simulated from the present climate. The range simulated for Scandinavia and Iceland dominates the pattern and is very similar in the two simulations. The principal differences are the disappearance from Scotland and reduction in number of simulated occurrences in central and southern Europe

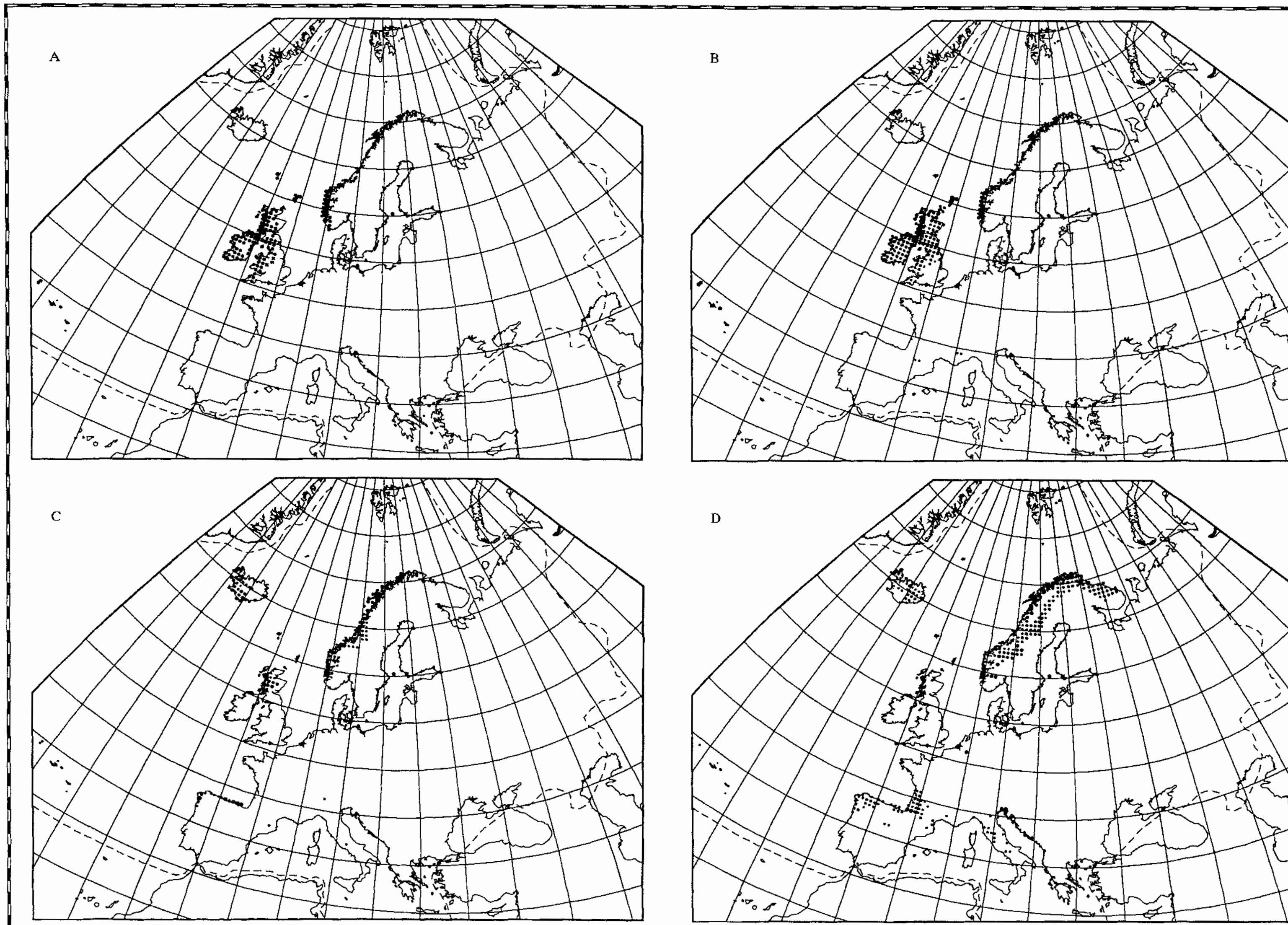

FIG. 18. *Hymenophyllum wilsonii* distributions. (a) Observed distribution (Jalas & Suominen, 1972); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.773$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.35; 69% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 90% of the observed occurrences being simulated.)

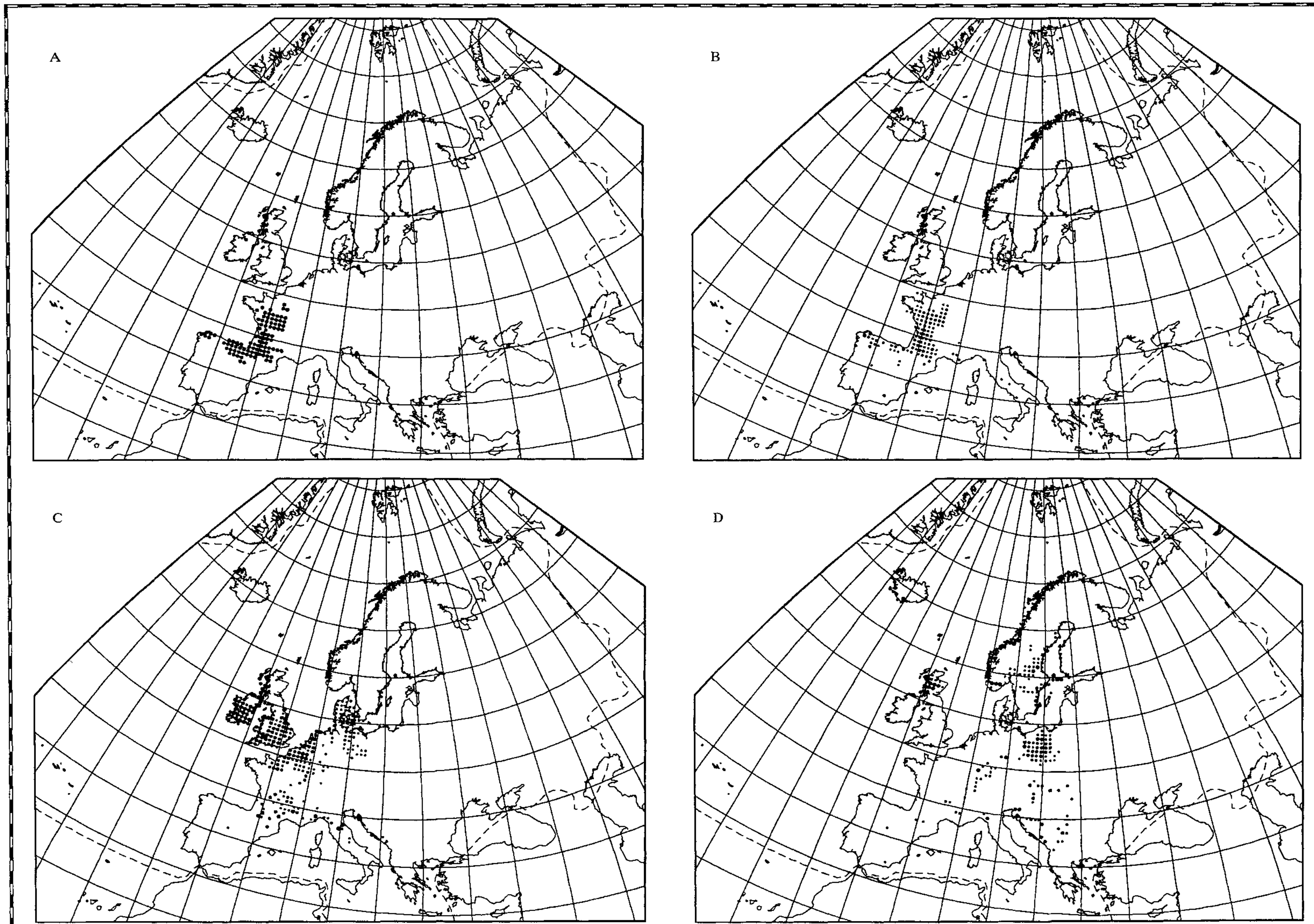

FIG. 19. *Erica vagans* distributions. (a) Observed distribution (compiled from various sources—see text); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.655$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.30; 61% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 73% of the observed occurrences being simulated.)

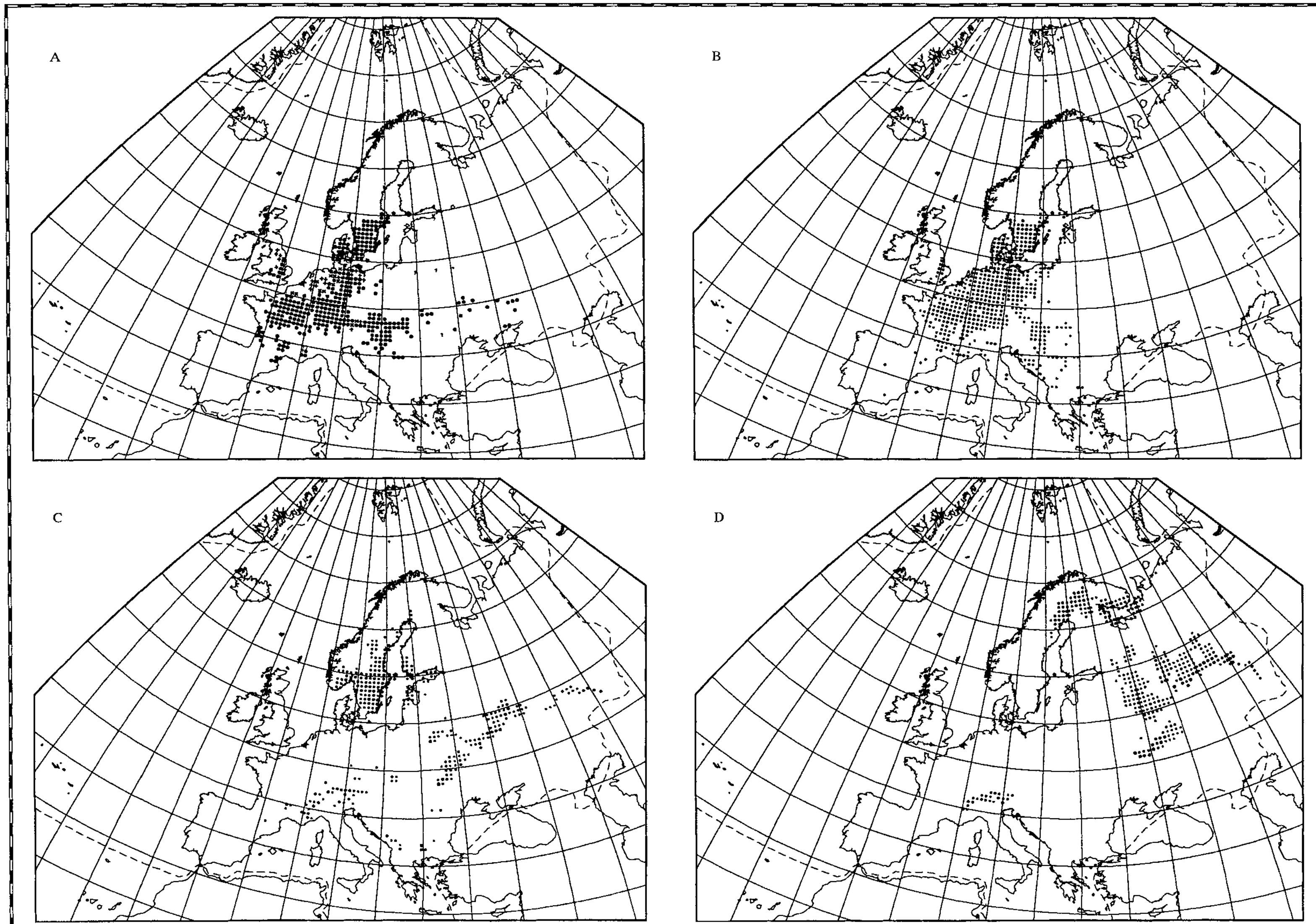

FIG. 20. *Pulsatilla vulgaris* distributions: (a) Observed distribution (Jalas & Suominen, 1989: combined distribution for *P. vulgaris* sspp. *vulgaris*, *gotlandica* and *grandis*); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.613$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.35; 58% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 75% of the observed occurrences being simulated.)

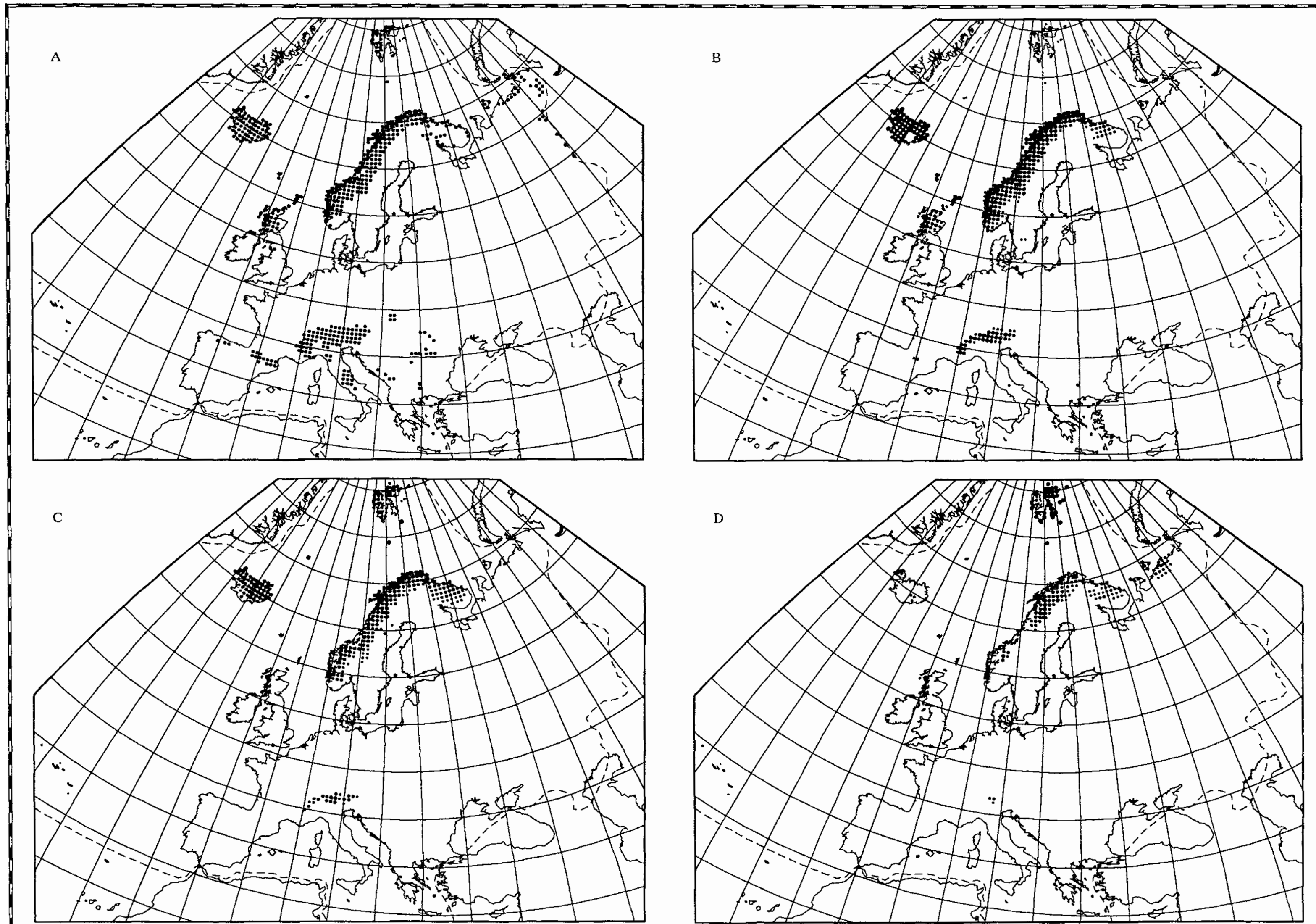

FIG. 21. *Silene acaulis* distributions. (a) Observed distribution (Jalas & Suominen, 1986); (b) distribution simulated using the response surface and the present climate ($\kappa = 0.708$); (c) distribution simulated for the OSU $2 \times CO_2$ scenario; (d) distribution simulated for the UKMO $2 \times CO_2$ scenario. (In simulated distributions, dots are scaled according to the simulated probability of occurrence; dots are shown for probabilities ≥ 0.40; 85% of the localities predicted in the simulation for the present climate correspond to observed occurrences, 65% of the observed occurrences being simulated.)

complemented by an increased number of simulated occurrences in Svalbard.

The range simulated for the UKMO $2 \times CO_2$ climatic scenario (Fig. 21D) shows further reduction in central Europe and decline in Iceland and southern Scandinavia.

DISCUSSION

Climate response surfaces

The degree of success with which the present ranges of the eight chosen species may be modelled using the three bioclimate variables selected strongly supports the hypothesis that species' overall geographical ranges are determined principally by the macroclimate. Furthermore, this hypothesis holds true even in Europe where the intensity of human disturbance of natural ecosystems has been considerable.

The use of climate response surfaces for this purpose has several advantages, amongst which we can emphasize:

(1) The response surface may be visualized (Figs 5–7, 9–13), aiding in understanding of the climatic constraints upon the overall range of the species and revealing the 'roughness' of the climatic response that may indicate the operation of other constraints upon the species' realised range (compare e.g. Figs 5 with 6 or 13 with 12). These other constraints may be imposed by other aspects of the environment, by interactions with other organisms, or by some combination of the two.

(2) The response surface provides a means by which the probability of occurrence of the species may be evaluated for any combination of values of the climate variables used to fit the surface. As with any other similar method, this will be most reliable when this combination lies within the range of combinations of values used to fit the surface. However, the use of the method of locally-weighted regression (Cleveland & Devlin, 1988) to fit and extrapolate the surfaces ensures that any extrapolation is performed conservatively; extrapolated probability values are asymptotic to the value at the fitted point that lies closest in the climatic space to the point to which the extrapolation is being made.

(3) The interacting effects of the two or three bioclimate variables can be modelled, c.f. Hintikka (1963); in this respect the approach offers a considerable advantage over most methods for defining 'climatic envelopes' that consider the bioclimate variables separately.

(4) The use of the grid of presences or absences to evaluate the probability of occurrence at given locations in the climate space offers a further advantage over methods that consider only overall climate envelopes that define presence *v*. absence. All of the species examined have shown areas of declining probability of occurrence within their overall climatic range such that a simulation of their range using a threshold probability of 0.01 would grossly exaggerate their realized range.

Simulated potential future ranges

The principal limitation upon the accuracy with which species' potential future ranges may be forecast lies in uncertainties about the future climate. Although the IPCC concluded that continued unrestrained emissions of greenhouse gases (their 'Business-as-Usual' scenario) would "result in a likely increase in global mean temperature of 1°C … by 2025 and 3°C before the end of the next century" (Houghton *et al.*, 1990 p. xi) this must be tempered by uncertainties about both the climate sensitivity to increasing levels of greenhouse gases and the resulting regional patterns of climate change. A variety of GCM simulations for greenhouse forcing equivalent to a doubling of the pre-industrial atmospheric concentration of CO_2 exhibit a range of climate sensitivities with the forecast global mean temperature increase varying between 1.5 and 4.5°C (Houghton *et al.*, 1990, 1992). Similar or even greater variations are seen when regional comparisons are made.

Given this uncertainty we have made simulations for two alternative GCM scenarios representing sensitivities near to the IPCC 'best guess' of 2.5°C global temperature increase (Houghton *et al.*, 1990, 1992) (OSU: (Schlesinger & Zhao, 1989) – 2.8°C global mean temperature increase and 8% increase in global precipitation) and at the upper end of the overall range (UKMO: (Mitchell, 1983) – 5.2°C global mean temperature increase and 15% increase in global precipitation). Our intention is to illustrate only the range of possible implications for species' ranges rather than to make *forecasts* of changes that might actually occur.

The results have been presented above as maps of the simulated distributions and are summarized in Table 1 in terms of the numbers of simulated occurrences and the proportion of the present ranges still occupied for the different scenarios. The most striking conclusion is the extent of the changes in range simulated even for the more moderate OSU scenario. Only for two species, *Picea abies* and *Silene acaulis*, do the simulated ranges for this scenario approach the same proportion of coincidence with the observed range as is seen for the simulation from the present climate; in all six other species there is marked reduction in the proportional coincidence between the simulation and the recorded range. Even in the two species for which the proportion of coincidence is maintained the reduction of the number of simulated occurrences for *P. abies* to less than 60% of the number for the present climate means that overall this species is much reduced. Of the eight species, three show a larger number of simulated occurrences for the OSU scenario than for the present climate (*Abies alba*, *Quercus ilex* and *Erica vagans*); of those that show decreased numbers of simulated occurrences, *Picea abies* is reduced by $>40\%$ and *Hymenophyllum wilsonii* by $>25\%$.

When the results for the UKMO scenario are examined then the same trend is apparent, although it is amplified as might be expected for this more extreme scenario. The same three species once again show an increased number of simulated occurrences when compared to the simulation for the present climate, although all three have fewer simulated occurrences than for the OSU scenario. The species exhibiting this tendency towards an expansion of their range are southern or south-western in present distribution. However, this potential to occupy an enlarged range must be tempered by the further reduced proportion of coincidence between the range simulated for the UKMO scenario and the recorded distribution; this drops as low as 0.004 for *Erica vagans* and is < 0.15 even for *Quercus ilex*. The oceanic *H. wilsonii* also now shows an increased number of simulated occurrences, although none coincides with a recorded occurrence.

Only one species, *P. abies*, continues to have a high proportion of coincidence between the range simulated for the UKMO scenario and the recorded range; this statistic obscures the fact that the total simulated range is reduced to less than 25% of that simulated for the present climate. *H. wilsonii*, as noted above, shows no coincidence between simulated occurrences and its recorded distribution. The situation for *Pulsatilla vulgaris* is only marginally better with the range reduced to *c*. 70% of the extent of that simulated for the present climate but only 1.1% of the simulated occurrences coinciding with recorded occurrences.

A final striking feature of the simulated potential ranges is that they show no similarity to the ranges occupied during the last interglacial in the case of those species for which a pollen record from that period is available (Watts, 1988). The suggestion made by some that the last interglacial might in fact represent an analogue for potential future conditions (Budyko & Izrael, 1987) thus seems most improbable.

Global change

Although, as we have emphasized above, the maps of simulated future potential ranges presented here do not represent *forecasts*, they do serve to provide an indication of the magnitude of the potential impact upon species' distributions and, hence, upon terrestrial ecosystem composition, structure and function. The species selected form a representative cross-section of the variety of distribution patterns and of range extents found in the European higher plant flora. The implications of the modelled potential range changes are that most, if not all, European higher plant species are likely to experience pronounced changes in the location and/or extent of their potential ranges in the event of climate changes of the magnitude simulated by GCMs for a doubling of the pre-industrial 'greenhouse effect'.

Relatively widespread species, exemplified here by *Picea abies* and *Tilia cordata*, are likely to suffer pronounced range reductions, although their future potential ranges generally will overlap with their present ranges. More restricted species may exhibit a variety of responses according to their present distribution patterns and climatic tolerances. Some southern and/or south-western species may experience a marked increase in the extent of their potential range (e.g. *Quercus ilex*, *Erica vagans*) whereas many northern or Arctic-Alpine species may suffer marked reduction of their potential range (e.g. *Silene acaulis*). Some relatively restricted species may experience little change in the overall extent of their potential range, although their potential future range may not overlap at all with their present range (e.g. *Hymenophyllum wilsonii*). Even those species that experience only limited range reduction or even modest range expansion may show little overlap between their future potential ranges and their present ranges (e.g. *Erica vagans*, *Pulsatilla vulgaris*).

The marked shifts seen for most of the species examined are unlikely to be realized within the timescales over which the simulated climate changes are expected to occur (Houghton *et al*, 1990, 1992). The rates of the expected climatic changes are more rapid than even the most rapid extensive changes during the recent geological past (Davis, 1986, 1990; Huntley, 1991). Consequently, plant species are unlikely to be able to achieve the migration rates necessary to maintain their ranges in equilibrium with the changing climate (Davis, 1986, 1990; Huntley, 1991). Thus, even those species that might be capable of range expansion under the new climate regime may be threatened with severe population reduction or even extinction if their future potential range overlaps their present range to only a limited extent. Those species that exhibit no overlap between their present and potential future ranges very likely may be threatened with extinction if such climatic changes do, in fact, take place. The only possible exception amongst the species examined is *Hymenophyllum wilsonii*; the dispersal of this species depends upon wind-dispersed spores that are produced in large quantities and that are capable of travelling very long distances. The remainder of the species depend for dispersal upon seeds that are unlikely to be dispersed over comparable distances to those achieved by spores.

Given the likelihood that many longer-lived species' distribution limits will not keep pace with the forecast climate changes and that ecosystems thus will not remain in equilibrium with climate, the transient impacts of climate change must be considered. Some ecosystems may be capable of persistence for so long as species that may be favoured in competition by the changed climate conditions lag in their migrations. In other cases, major ecosystem components may be unable to persist under the changed conditions; opportunist, early-successional species then may replace these species until such time as the late-successional species favoured by the new climate conditions are able to migrate into the region. Without detailed autecological understanding of the mechanisms underlying observed climatic limits the outcome for any particular ecosystem cannot readily be predicted.

The latitudinal extent of some of the simulated range displacements leads to the further possibility that some species photoperiodic requirements may prevent them from realising the range shifts necessary to maintain equilibrium with climate conditions. Given that the forecast combinations of latitude and climate apparently have no analogue in the recent geological past of the Quaternary or late-Tertiary, during which time most, if not all, present European species have evolved, it is likely that many species will lack the genetic capability to adapt to these new combinations of conditions.

Even supposing that plant species were able to achieve the range shifts necessary to occupy their future potential ranges, the implications with respect to biogeographic patterns and to ecosystem conservation are profound. In addition to the effects that we have examined, the increased atmospheric concentration of CO_2 will potentially have further direct effects upon some species and may influence the way in which climate determines their range limits. This especially will be true of range limits determined by drought sensitivity because the water use efficiency of many species is enhanced when exposed to higher than ambient CO_2 concentrations. This effect is unlikely to have any marked impact upon our conclusions, however, because the principal determinant of the shifts in range that we have modelled is the change in temperature; even under the more extreme UKMO scenario the AET/PET values are not reduced in most parts of Europe.

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