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TREE SPECIES' RESPONSES TO ENVIRONMENTAL CHANGES DURING THE LAST GLACIAL: EVALUATING ALTERNATIVE HYPOTHESES USING A SPATIALLY-EXPLICIT MIGRATION MODEL*

B. Huntley (1) **- Y.C. Collingham** (1) **- M.O. Hill** (2)
(1)Environmental Research Centre, University of Durham, Dept. of Biological Sciences, Durham, U. K.
(2)Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, U. K.

RIASSUNTO - *Risposta di specie arboree ai cambiamenti ambiantali nel corso dell'ultimo glaciale: valutazione di ipotesi alternative mediante il modello MIGRATE* - Il Quaternario *Italian Journal of Quaternary Sciences*, 9(2), 1996, 617-626 - Il modello MIGRATE viene impiegato per una serie di simulazioni sulla risposta di specie arboree a rapidi mutamenti ambientali. Vengono esaminate due forme alternative della distribuzione iniziale, che influiscono sulla disponibilità di *habitat* e sulle caratteristiche riporduttive e di dispersione delle specie, rispettivamente. I risultati forniscono una base per la valutazione critica della forma di distribuzione dei rifugi glaciali in una regione. Le simulazioni forniscono inoltre un sostegno all'ipotesi che le specie mesiche dell'Italia centro-meridionale erano in grado di rispondere alle rapide fluttuazioni ambientali durante l'ultimo periodo glaciale perché, durante i periodo meno favorevoli, esse occupavano numerosi rifugi dispersi nel territorio in micro-ambienti favorevoli. Da questi potevano, poi, espandersi rapidamente durante intervalli di tempo, anche brevi, con condizioni ambientali relativamente favorevoli.

ABSTRACT - *Tree species' responses to environmental changes during the last glacial: evaluating alternative hypotheses using a spatially-explicit migration model* - Il Quaternario *Italian Journal of Quaternary Sciences*, 9(2), 1996, 617-626 - The MIGRATE model has been used to perform a series of simulations of the response of trees to rapid environmental changes; two alternative forms of initial distribution have been examined, as have the influences of habitat availability and the reproductive and dispersal characteristics of the trees. The results provide a basis for a critical test of the form of the glacial refugial distributions of trees in a region. They also provide strong support for the hypothesis that mesic trees in southern Italy were able to respond to the rapidly fluctuating environment of the last glacial because, during unfavourable periods, they occupied numerous scattered refuges in suitable microhabitats within the landscape. They then could expand rapidly across the landscape during even short intervals of relatively favourable conditions.

Keywords: Refugia, pollen, migration, modelling, Italy
Parole chiave: Rifugio, polline, migrazione, modello, Italia

1. INTRODUCTION

Two contrasting forms of response by trees to Quaternary climate changes have been proposed. In eastern North America and in Europe palynological data for the period since the last glacial maximum have been used to draw isochrone and/or isopoll maps (Davis, 1976; 1983; Huntley, 1988; Huntley & Birks, 1983; Jacobson *et al.*, 1987; Webb, 1981; 1987; 1988) that portray tree populations undergoing continental-scale migrations. The poleward range limits of many individual taxa shifted north by >2000 km as a consequence of the transition from the last glacial to the Holocene; other taxa showed principally east-west range limit shifts. Whereas for many taxa their post-glacial migration resulted in an overall increase in the extent of their geographical distribution, for others the net effect was a shift of distribution without any substantial change in their area of occurrence. Independent estimates of the rates at which species' range limits advanced during these migrations have provided closely similar results from eastern North America, Europe and Japan (Davis, 1976; Huntley, 1988; 1989; Huntley & Birks, 1983; Huntley & Webb, 1989); for most taxa these estimates give values of 200-500 m yr^{-1}, although exceptionally rates of 1-2 km yr^{-1} have been reported (Huntley, 1988; Huntley & Birks, 1983; Ritchie & MacDonald, 1986).

Such large-scale migrations are not always possible, however. The islands of New Zealand represent an extreme example of a situation where insularity precludes migration over such distances, yet these islands were subject to substantial climatic changes during the last deglaciation and the palynological record shows "changes similar in magnitude to those from continental regions" (McGlone *et al.*, 1993 - p. 294). McGlone (1988) described a series of features of the post-glacial reafforestation of New Zealand, including its rapidity (less than 400 yr to complete the process, not only at individual localities but apparently also regionally) and the lack of any evidence for the controlling influence of environmental gradients on the timing and rate of the reafforestation. These characteristics led him to hypothesise that "forest species survived the glacial maximum in numerous, scattered, small areas, which each may have contained no more than a handful of large trees. These provided .... nuclei from which the forest spread with very great rapidity across the landscape" (McGlone, 1988 - p. 585). He noted also that the biological charac-

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teristics of some tree species were such as to be likely "to preclude marginal spread rapid enough to give near simultaneous afforestation" (McGlone, 1988 - p. 585). This led him to reject the alternative hypothesis that the tree species had survived the glacial in "few, necessarily small, refugia hugging the glacial coastline" (McGlone, 1988 - p. 586).

An hypothesis of scattered, small populations requires that the landscape offers a diversity of habitats that may accommodate taxa of widely differing tolerances; this is likely to be possible only in areas of high relief such as New Zealand. Furthermore, although slopes of varying aspect may offer some scope for amelioration of high temperature extremes, and can greatly alter the annual temperature sum as well as the available solar radiation, they cannot generally provide escape from low temperature extremes. Varied topography can, however, provide relief from water shortage, both in terms of available soil moisture and atmospheric humidity, as well as providing dry habitats in a generally oceanic climate *régime* such as that of New Zealand. It may be relevant in this respect that the estimated mean temperature for the last glacial maximum in New Zealand was only 4·5-5·0°C cooler than present (McGlone *et al.*, 1993). The widespread absence of forest cover in the lowlands thus cannot be attributed to an overall prevalence of cold conditions; instead it is ascribed to a combination of drought, strong winds and periodic invasions of polar air masses that would result in short periods with temperatures much colder than the mean, even in summer (McGlone *et al.*, 1993). This is in contrast to north-west Europe, where temperatures at the last glacial maximum, and even at the end of the glacial, have been reconstructed to have been as much as 25°C cooler than today, at least in winter (Atkinson *et al.*, 1987; Huntley, 1994).

Elsewhere, in other high relief areas, trees may have behaved in a similar manner to that hypothesised for New Zealand and, as a result, may have been able to respond much more rapidly to climatic changes than could trees whose response involved spatially-extensive migrations. Changes toward more favourable conditions would elicit rapid population expansion from the many refugia, whereas revertence to unfavourable conditions quickly would eliminate once again all but those small parts of the population that were occupying microhabitats that provided relief from the particular unfavourable conditions that now prevailed. Such rapid responses of vegetation to late-glacial climate fluctuations have been reported for Chile (Markgraf & Kenny, 1996), whilst Watts *et al.* (1996a) and Huntley *et al.* (1996a) have reported extremely rapid responses of forest cover in southern Italy to rapid climate fluctuations during the last glacial stage. Both Chile and southern Italy are areas of high relief. In addition, a significant part of the climate fluctuation recorded in these studies is interpreted as variations in moisture *régime* (Markgraf & Kenny, 1996; Watts *et al.*, 1996a). Thus it is plausible that the same pattern of tree distribution during unfavourable periods as has been hypothesised for New Zealand might have applied also in these regions and that this may account for the rapidity of the observed responses to climate fluctuations.

In order to test the hypothesis advanced by McGlone (1988; 1996), it is necessary to determine whether the location and character of populations of trees during unfavourable periods may influence the speed, and perhaps also the population dynamics, as reflected by the palynological record, of their response to a climate change that leads to a period of favourable conditions. Although, in principle, numerous palynological studies might be carried out across a region in order to examine the distribution of trees during unfavourable periods, this approach suffers from two practical limitations:

1 - The likelihood of obtaining evidence of isolated, small refugial populations of trees in this way is extremely small; given that to do so requires the study of many relatively small basins with localised pollen catchments (Jacobson & Bradshaw, 1981) the effort involved also is quite impractical.

2 - In the case of Italy at least, and probably also in other comparable areas of high relief, the number of suitable basins from which sediments may be obtained upon which to perform palynological studies is severely limited and precludes this approach to the location of refugial populations of trees.

The only practical approach available to address this problem is through the application of a simulation model. MIGRATE (Collingham, 1995; Collingham *et al.*, 1996; Huntley *et al.*, 1996b) is a suitable model to apply in this case. This model is spatially explicit and has been developed specifically to simulate the migration of tree populations across heterogeneous landscapes. We have used this model to carry out a series of simulations for alternative forms of refugial distribution of a tree with the general life-history characteristics of *Tilia cordata.* We have chosen to simulate the response of the tree population to a climatic fluctuation, *i.e.* a change from initially unfavourable to favourable conditions followed, after a period of stability, by revertence to unfavourable conditions once again. The results of the simulations have been evaluated in terms of the rapidity of the observed response and also in terms of the observed form of the population growth and subsequent decline within an area chosen to represent the pollen catchment of a moderate-sized lake comparable to Lago Grande di Monticchio (Huntley *et al.*, 1996a; Watts *et al.*, 1996a; Watts *et al.*, 1996b).

2. THE SIMULATIONS

MIGRATE is a single-species grid-based model; the characteristics of each cell of the grid, in particular its 'suitability' (*i.e.* how successful the species is likely to be in growing and reproducing, given *e.g.* the climatic, soil, and other conditions prevailing in that cell) and 'habitat availability' (*i.e.* the extent of suitable habitat, *e.g.* deciduous woodland for a deciduous tree, wetland for species demanding of waterlogged soils, etc. in that cell) for the species being simulated, may be specified. This enables simulations of migration across realistically heterogeneous landscapes to be carried out (Collingham, 1995; Collingham *et al.*, 1996; Griffin, 1994). A variety of aspects of the environment may be overlaid onto the

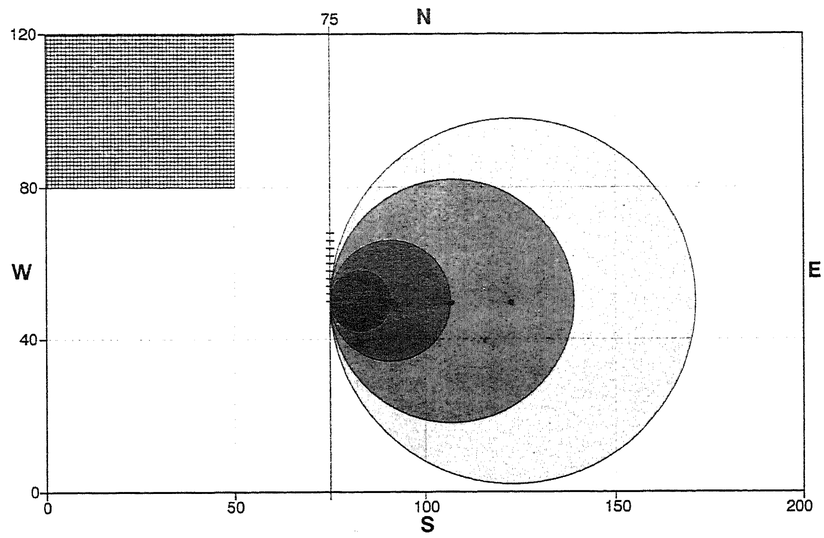

Fig. 1 - Schematic diagram of the model grid. The overall grid is shown, although with the individual cells indicated only for a segment in the north-west corner. The vertical line 75 km from the western margin forms a tangent to the pollen catchments of the lakes used to represent the results of the simulations. The catchments of the 10 replicate lakes of each size meet the line respectively at the ten tick marks shown; the southernmost lake is centred 50 km from the southern margin of the grid and subsequent lakes lie at 2 km intervals northward. The 5 differentially shaded circles show the catchments of the southernmost lakes of each size, the position of the centre of the lakes being indicated by black dots.

Diagramma schematico della griglia del modello. La figura mostra la griglia, anche se le celle individuali sono indicate solo per un segmento nell'angolo nord-occidentale. La linea verticale 75 km dal margine occidentale è la tangente al bacino di cattura del polline dei laghi utilizzati per rappresentare i risultati delle simulazioni. I bacini di cattura dei dieci laghi replicati di ciascuna dimensione incontrano la tangente in corrispondenza delle dieci tacche. Il lago più meridionale si trova a 50 km dal bordo meridionale della griglia ed gli altri laghi si collocano ad intervalli di 2 km in direzione nord. I cinque cerchi a differente retinatura indicano i bacini di cattura dei laghi più meridionali di ciascuna dimensione; la posizione del centro dei laghi è indicata dai punti in nero.

model grid and used to derive the suitability and habitat availability values for the grid cells.

In the simulations reported here we used an artificial rectangular grid of 200 x 120 1 km square cells (Fig. 1). The dimensions of this grid were chosen so as to provide an area similar to that required to encompass more or less centrally the pollen catchment of Lago Grande di Monticchio whilst extending to the Adriatic and Tyrrhenian coasts as they might have been during glacial times. We have manipulated the product of suitability and habitat availability, which we refer to as 'carrying capacity', of cells in the grid so as to represent either 'favourable' or 'unfavourable' conditions for the tree. Under unfavourable conditions we have considered two alternative distributions of 'refugial' grid cells corresponding either to the 'McGlone hypothesis' of scattered small populations throughout the domain of the model (Unfavourable A) or to an hypothesis of a discrete marginal refuge for a larger population (Unfavourable B). Under favourable conditions we also have considered two alternative situations so as to evaluate sensitivity to the proportion of the landscape that becomes available; in the first situation (Favourable 1) a high proportion of grid cells are available to the tree, whereas in the second (Favourable 2) a much smaller proportion of grid cells are available. The characteristics of the four grids used are given in Table 1.

All of the simulations were initiated with the same initial number of trees 'seeded' into an unfavourable grid. The grids were seeded either with 240 scattered populations each of 400 trees (Unfavourable A), or with 96,000 trees shared evenly between the eight cells of the marginal refuge (Unfavourable B). The simulations then were run for 5 generations with the unfavourable grid. So as to represent a rapid environmental change, comparable to those that have been inferred from $\delta^{18}O$ records in ice cores (Dansgaard *et al.,* 1989; GRIP Members, 1993), the unfavourable grid then was replaced by a favourable grid within the space of a single generation. In each simulation the available cells in the favourable grid included those that had been available in the preceding unfavourable grid, the additional cells being selected randomly. The simulations then were run for a further period of sufficient generations to allow the populations of trees to stabilise within the pollen catchment areas of a series of lakes located such that their catchments extended eastwards from the grid line 75 km from the western margin of the grid (Fig. 1). So as to examine the form of the population decline during a change toward unfavourable conditions the grid now was reverted to the unfavourable 'A' state progressively over 5 generations and the model run for a further 4 generations thereafter. The reversion of the grid was performed by random

Table 1 - Characteristics of the unfavourable and favourable grids.

Caratteristiche delle griglie sfavorevoli e di quelle favorevoli.

Grid type and name	**Proportion of cells available to the tree**	**Carrying capacity of the available cells**	**Distribution of the available cells**
Unfavourable A - 'scattered'	0·01	0·02	random
Unfavourable B - 'discrete refuge'	0·000333	0·6	discrete block of 8 cells at 'western' margin and centred on 60 km 'north'
Favourable 1 - 'high density'	0·7	0·8	random
Favourable 2 - 'low density'	0·3	0·8	random

deletion of available cells coupled to reductions in carrying capacity of those remaining. The unfavourable 'A' grid was used in all of the simulations so as to reflect the likely realistic situation in which at least initially the population would become fragmented, with small sub-populations persisting for some time in favourable parts of the landscape. The characteristics of the four intermediate grids for the reversions from each of the two alternative favourable grids are given in Table 2.

Table 2 - Characteristics of intermediate grids used during revertence to unfavourable conditions.

Caratteristiche delle griglie intermedie usate per la regressione a condizioni sfavorevoli.

Grid name	Carrying capacity of the available cells	Proportion of cells available to the tree	
		Reverting from Favourable 1	Reverting from Favourable 2
Reversion - Step 1	0·644	0·562	0·242
Reversion - Step 2	0·488	0·424	0·184
Reversion - Step 3	0·332	0·286	0·126
Reversion - Step 4	0·176	0·148	0·058

MIGRATE requires a series of parameters to be specified that relate to the general biological and life-history attributes of the species being simulated; these include such things as the area occupied by a mature individual, the time taken to reach reproductive maturity, the number of propagules produced by an individual and the survival probability of an individual. In order to perform simulations for long-lived species that exhibit differing survival probabilities and propagule outputs at different stages of their life-history, the model considers the population as a whole to be comprised of a series of cohort classes, each of which separately is assigned values for survival and propagule output. In our simulations the population was considered to fall into only 2 cohort classes, pre-reproductive trees and mature trees of reproductive age. Note that the propagule output of the first cohort (S_1 - see Table 3) is not zero because a proportion of those trees that initially are in the pre-reproductive cohort will have matured and begun to reproduce within the time step of the model. One further feature also was required in the version of the model used in our experiments. As a favourable grid was reverted to an unfavourable grid an increasing number of grid cells contained an excess of mature individuals compared to their carrying capacity under the new conditions. Because this progressive shift toward an unfavourable grid was intended to represent a gradual deterioration of environmental conditions that rendered an increasing proportion of the cells unsuitable for the tree, it was deemed inappropriate that the excess trees should continue to have the same survival probability as previously. Therefore, that proportion of the trees in any grid cell that was in excess of the carrying capacity of the cell was assigned a survival probability half that of the remainder of the cohort of mature trees.

Table 3 - Parameter values used for the MIGRATE simulations.

Parametri usati per le simulazioni MIGRATE.

	Value		
Parameter	Case I	Case II	Definition
a	50 m^2	50 m^2	Area occupied by a mature individual
T	25 yr	25 yr	Time to reach reproductive maturity (*i.e.* generation length)
S_1	$8{\cdot}32 \times 10^4$	$8{\cdot}32 \times 10^4$	Number of propagules produced in 1 generation length by 1 individual of the1st cohort
S_2	$1{\cdot}6 \times 10^5$	$1{\cdot}6 \times 10^5$	Number of propagules produced in 1 generation length by 1 individual of the 2nd cohort
P_0	$0{\cdot}25 \times 10^{-3}$	$0{\cdot}1 \times 10^{-4}$	Probability of a propagule establishing an offspring that survives to maturity in the absence of self-thinning
P_1	0·913	0·913	Probability of a mature individual surviving a further interval of 1 generation length in a favourable environment
P_2	0·4565	0·4565	Probability of a mature individual surviving a further interval of 1 generation length in a deteriorating environment when the carrying capacity is exceeded
P_{loc}	0·99	0·90	Probability of local dispersal
R_{loc}	0·2 km	0·2 km	Root-mean-square displacement for local dispersal
P_{long}	0·01	0·10	Probability of long-distance dispersal
R_{long}	9·7 km	45 km	Root-mean-square displacement for long-distance dispersal

Propagule dispersal is represented in MIGRATE by a mixture of two bivariate normal distributions; most propagules are dispersed locally according to a distribution with a relatively small root-mean-square displacement, but a small proportion are dispersed over longer distances according to an alternative distribution that has a larger root-mean-square displacement. In order to investigate the effects of the extent of long-distance dispersal upon our simulations, two alternative cases were examined. In Case I a small proportion of propagules was dispersed over only moderate distances, whereas in Case II a larger proportion of propagules was dispersed over a longer distance. In order to maintain similar overall migration rates in the two cases it also was necessary to vary the probability of a propagule maturing in the absence of self thinning (P_0 - see Table 3) (Collingham *et al.*, 1996); thus the 'fecundity', *i.e.* the number of offspring surviving to maturity per individual per generation ($F = S_2 \times P_0$ for the mature cohort), was greater in Case I than in Case II. Migration rates for the two cases were compared using simulations of the spread of the tree across homogeneous grids offering the same overall carrying capacity as each of the two favourable grids. For a homogeneous landscape in which all cells had a carrying capacity of 0·56 (equivalent to Favourable 1) the Case I parameters gave a migration rate of 270 m yr^{-1}, whereas for Case II the rate was somewhat faster at 410 m yr^{-1}. For a homogeneous landscape of carrying capacity 0·24 (equivalent to Favourable 2) the migration rates converged to values of 190 and 200 m yr^{-1} for Case I and Case II, respectively. These simulations also confirmed that the two alternative sets of dispersal parameters gave simulated mean migration rates comparable in general magnitude to migration rates estimated from the fossil record (Huntley & Birks, 1983). All of the parameter values used in our simulations are given in Table 3.

During the course of a simulation the model keeps track of the numbers of individuals of each cohort present in each cell of the grid as well as of the number of

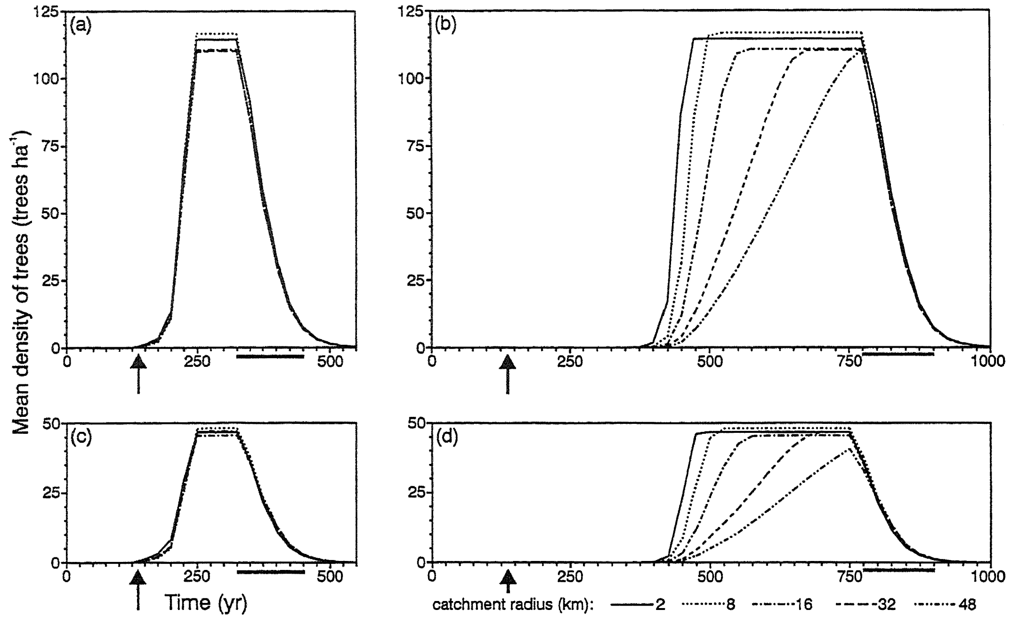

Fig. 2 - Results of the simulations using Case I parameters. a) Simulation for Unfavourable A transformed to Favourable 1, reversion commencing after generation 13 (325 yr); b) Simulation for Unfavourable B transformed to Favourable 1, reversion commencing after generation 31 (775 yr); c) Simulation for Unfavourable A transformed to Favourable 2, reversion commencing after generation 13 (325 yr); and d) Simulation for Unfavourable B transformed to Favourable 2, reversion commencing after generation 31 (775 yr). In all simulations the transformation from the unfavourable to the favourable grid took place in the interval 125-150 yr (marked by an arrow); the period of reversion is indicated by a bar. In each case the five curves shown represent the mean of the results simulated for 10 lakes with a given pollen catchment radius (see text).

Risultati delle simulazioni se si utilizzano i parametri del Caso I. a) Simulazione per Non Favorevole A che si trasforma in Favorevole 1, con rovesciamento che inizia dopo la 13a generazione (325 anni); b) Simulazione per Non Favorevole B che si trasforma in Favorevole 1, con rovesciamento che inizia dopo la 31a generazione (775 anni); c) Simulazione per Non Favorevole A che si trasforma in Favorevole 2, con rovesciamento che inizia dopo la 13a generazione (325 anni); d) Simulazione per Non Favorevole B che si trasforma in Favorevole 2, con rovesciamento che inizia dopo la 31a generazione (775 anni). In tutte le simulazioni la trasformazione di una griglia da Non Favorevole a Favorevole si svolge nell'intervallo 125-150 anni (indicato da una freccia); il periodo di rovesciamento è indicato da una barra. In ciascun diagramma le 5 curve rappresentano la media dei risultati simulati per 10 laghi ciascuno dei quali con un dato raggio di cattura del polline (vedi il testo).

propagules present in each cell following their dispersal. For the purposes of simulating dispersal all individuals notionally are located at the centre of the grid cell in which they occur. We performed a total of eight simulations, combining each of the two unfavourable grids with each of the two favourable grids for each of the two alternative dispersal parameter cases.

3. RESULTS

The results of the eight simulations are presented graphically in a form that is intended to enable meaningful comparisons to be made with pollen abundance curves. For each simulation the results are presented as they might be recorded by the pollen reaching the sediments of lakes of five different sizes and hence pollen catchment radii; the pollen catchments used are circular with radii of 2, 8, 16, 32 and 48 km respectively. For each size of pollen catchment ten replicate lakes were sampled, centred at different distances northwards across the grid; the first was at 50 km and each subsequently was a further 2 km north. All of the lakes were positioned so that the western boundary of their pollen catchment fell 75 km from the western margin of the grid (Fig. 1); this ensured that in simulations using 'Unfavourable B' the migrating front of trees reached the boundary of the different sized pollen catchment areas in the same generation. At each generation of each simulation the total number of trees growing in the grid cells that fell within each pollen catchment was calculated and transformed into a mean density of trees within that pollen catchment, expressed in trees ha^{-1}; an overall mean value then was calculated from the ten replicate lakes of each size.

These mean density values have a simple monotonic relationship to the relative quantity of pollen of the tree species that would reach the lake; although they could be transformed into pollen accumulation rates using a model such as that of Davis & Sugita (1996), we have chosen for simplicity to plot the simulated tree abundances directly. They have been plotted against time elapsed since the beginning of the simulation and the resulting curves are presented in Figures 2 and 3. For comparison, Figure 4 illustrates a section of the curve for the abundance of tree pollen during the last glacial stage from the pollen record at Lago Grande di Montic-chio (Watts *et al.*, 1996a); this shows a series of examples of rapid increases and subsequent decreases of tree pollen abundance that are interpreted as responses to fluctuations in both temperature and moisture availability.

The first contrast between the simulations made using unfavourable grids 'A' and 'B' one could have predicted; it relates to the lag between the simulated environmental change toward favourable conditions and its manifestation as an increase in tree density within the pollen catchments (Figs. 2a *vs* b; 2c *vs* d). This lag reflects the period of time required by the tree to migrate from a discrete refuge at the edge of the grid into the

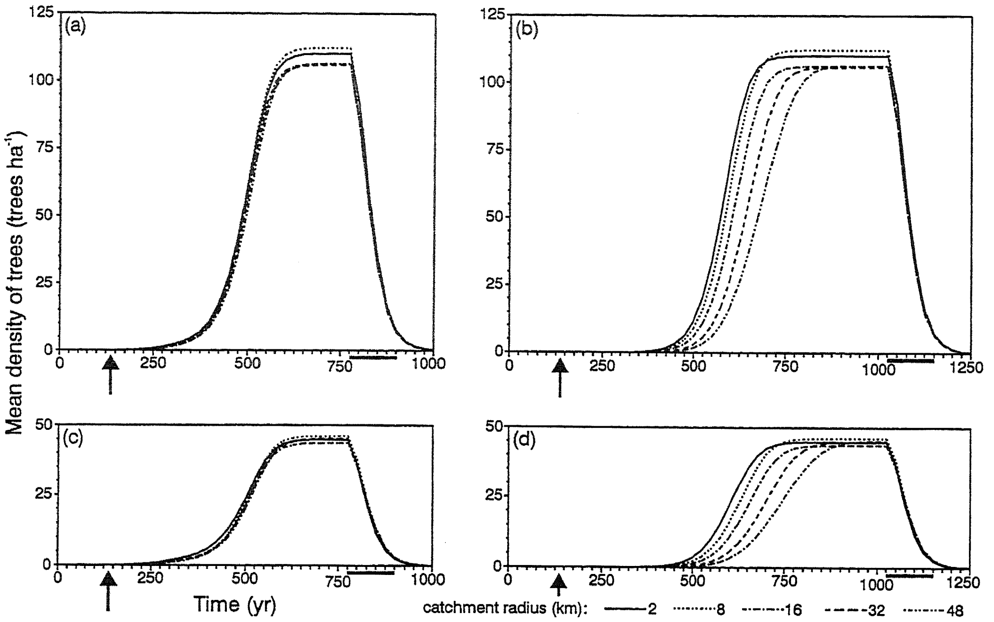

Fig. 3 - Results of the simulations using Case II parameters. a) Simulation for Unfavourable A transformed to Favourable 1, reversion commencing after generation 31 (775 yr); b) Simulation for Unfavourable B transformed to Favourable 1, reversion commencing after generation 41 (1025 yr); c) Simulation for Unfavourable A transformed to Favourable 2, reversion commencing after generation 31 (775 yr); and d) Simulation for Unfavourable B transformed to Favourable 2, reversion commencing after generation 41 (1025 yr). In all simulations the transformation from the unfavourable to the favourable grid took place in the interval 125-150 yr (marked by an arrow); the period of reversion is indicated by a bar. In each case the five curves shown represent the mean of the results simulated for 10 lakes with a given pollen catchment radius (see text).

Risultati delle simulazioni nel caso si utilizzino i parametri del Caso II. a) Simulazione per Non Favorevole A trasformato in Favorevole 1, con rovesciamento che inizia dopo la 31a generazione (775 anni); b) Simulazione per Non Favorevole B trasformato in Favorevole 1, con rovesciamento che inizia dopo la 41a generazione (1025 anni); c) Simulazione per Non Favorevole A trasformato in Favo-revole 2, con rovesciamento che inizia dopo la 31a generazione (775 anni); e d) Simulazione per Non Favorevole B trasformato in Favorevole 2, con rovesciamento che inizia dopo la 41a generazione (1025 anni). In tutte le simulazioni, la trasformazione da griglia non favorevole a griglia favorevole è avvenuta nell'intervallo di tempo 125-150 anni (indicato da una freccia); il periodo di tempo del rovesciamento è indicato da una barra. In ciascun diagramma le cinque curve rappresentano la media dei risultati simulati per 10 laghi, ciascuno dei quali avente un dato raggio di cattura del polline (vedi testo).

pollen catchment; in the present case the lag is relatively short, it requiring only ca. 250 years (*i.e.* 10 generations) for the tree to complete its migration from the marginal refuge to the edge of the lake catchments. The scattered small populations are in contrast able to respond without lag to the simulated environmental change, as McGlone (1988) hypothesised. This has implications for the minimum duration of environmental fluctuation that might elicit a response that could be sensed at pollen sites throughout a region.

The second contrast between the results was not one that had been predicted. Although McGlone did not explicitly consider the relative rate of increase of the tree population for the two alternative refugial distributions, he did expect the scattered refuges to result in the forest spreading "with very great rapidity across the landscape" (McGlone, 1988 - p. 585). Implicitly, the rate of increase of the tree population was expected to be greater from scattered refuges. This is not in fact the case; the local rate of population increase principally is determined by the life-history characteristics of the tree, in particular by its fecundity. Thus, whether increasing from scattered local refuges or from the first scattered individuals arriving as the result of long-distance dispersal of propagules from an advancing population front migrating from a distant refuge, the local rate of population increase will be the same; in the present simulations this is seen to be the case when we compare the four population curves for the lakes with the smallest pollen catchment in Figure 2. However, when we contrast these curves with the equivalent curves in Figure 3 we find that the latter are much more markedly 'S-shaped' with a markedly less steep maximum gradient. This reflects the 25-fold difference in fecundity between the Case I and Case II parameters (the mature cohort having fecundity values of 40 and 1·6 respectively). A notable consequence of the reduced fecundity in Case II is seen in cases where the initial distribution was in numerous scattered refuges. There now is a lag of ca. 10 generations before the populations begin their phase of most rapid increase; this lag is comparable to that of ca. 13 generations seen in cases where expansion was from a discrete marginal refuge (Figs. 3a *vs* b; 3c *vs* d).

The third point of contrast relates to the markedly differing patterns and rates of colonisation of the pollen catchment of a lake when comparing the two initial refugial states; this contrast is especially noticeable in the case of larger lakes. Tree populations expanding from numerous scattered refuges will enter the catchment from many different directions; some refuges may even be located within the catchment. In contrast, a tree population expanding across the landscape from a distant refuge will enter first at one side of the pollen catchment of the lake and then will progressively occupy the available habitat within that catchment. As Davis & Sugita (1996) have shown, such progressive occupation of the circular pollen catchment of a lake by a taxon advancing as a migrating front results in an 'S-shaped' growth curve

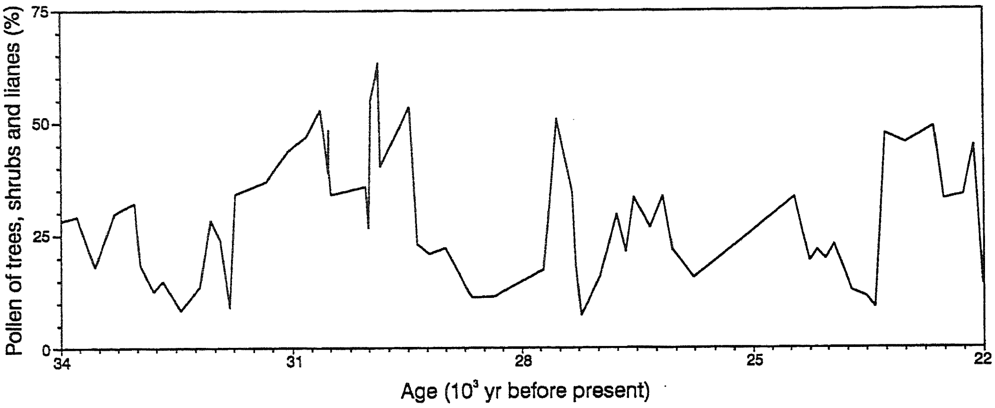

Fig. 4 - Pollen curve from Lago Grande di Monticchio. A section of the pollen abundance curve for trees, shrubs and lianes during the last glacial stage showing the frequent rapid changes in abundance of pollen of woody taxa recorded at this site.

Diagramma pollinico del Lago Grande di Monticchio. Viene riportato un tratto della curva di abbondanza per le specie arboree, arbustive e liane durante l'ultima fase glaciale che mostra i frequenti e rapidi cambiamenti in abbondanza del polline dei taxa *delle specie legnose registrati in questo sito.*

for the population within the catchment. The slope of the curve during the phase of most rapid increase, however, depends upon the size of the catchment and hence, in turn, upon the size of the lake (Figs. 2b and d). The pollen catchment of a small lake will be occupied by the advancing species relatively rapidly compared to that of a larger lake; thus the apparent maximum rate of increase of the tree population will be less for larger lakes (Davis & Sugita, 1996). This contrasts with the situation where the trees are expanding from many scattered small populations; in such cases no difference is observed amongst the maximum gradients of the curve of population growth within the catchments of the five lakes considered (Figs. 2a and c). The absence of any effect of lake size in these simulations indicates that lakes of markedly different sizes have a similar ability to record rapid increases in tree populations if the initial populations are small and scattered. Therefore, lakes of very different sizes are equally able to record the response of vegetation to rapid environmental changes, but only if the taxa were present in numerous small populations in favourable microhabitats prior to the change to more generally favourable conditions.

The form of the curve of population growth within the catchment also is sensitive to differences amongst species in their dispersal characteristics. In particular, the depth of the migrating front of a species expanding from a discrete refuge is determined both by the fecundity of the species and by the form of its dispersal curve (Collingham *et al.,* 1996). For any given migration rate the depth of the migration front primarily is determined by the combination of fecundity and dispersal characteristics that result in this particular rate. A species of relatively low fecundity can maintain a given migration rate if it achieves sufficiently long-distance dispersal of its propagules and in this case its migration front will have a much increased depth compared to that of a more fecund species the propagules of which are not dispersed over such great distances. In the simulations presented here the Case I parameters result in a migration front depth of ca. 15 km, whereas for the Case II parameters the depth is ca. 150 km. The depth of the migration front in turn determines the form of the curve of population increase within the pollen catchment of a lake for a species expanding from a discrete refuge. A species with a deep migration front will exhibit a more gradual onset of population increase than will a species with a shallow migration front. It is largely for this reason that the lag in reaching the lake catchments in Case II coincidentally more or less equates to the local lag in the rate of population increase reaching its maximum. This effect also accounts for the much reduced sensitivity to pollen catchment size of the maximum rate of increase within the catchment in simulations using the Case II parameters (Figs. 3b & d *vs* 2b & d); the rate now is primarily determined by the depth of the migration front which is much greater even than the diameter of even the largest catchments examined.

Of course the pollen-dispersal characteristics of the species also will influence how the population of trees is sensed by the lake. Davis & Sugita (1996) have shown that more widely-dispersed pollen taxa exhibit a more gradual onset of the increase in their pollen abundance values. To what extent this is true for species expanding from numerous scattered small populations as opposed to an advancing migration front has not to our knowledge been tested explicitly. On the basis of our results, plus those characteristics of an advancing front that lead to the observation of an 'S-shaped' curve of increasing pollen abundance values (Davis & Sugita, 1996), we would predict that a gradual onset of the increase in pollen abundance values would not be observed in cases where a taxon with widely-dispersed pollen was expanding from numerous scattered small populations.

Our simulations also illustrate the decline in a tree population as conditions revert toward those unfavourable for the taxon. Given that the characteristics of such a decline principally are determined by the survival probability of the mature individuals, no differences were expected or observed between the different simulations. What is striking, however, is that only a halving of the survival probability was necessary to produce rapid population decreases in response to the deteriorating environment. The deterioration spanned 125 yr and the simulations were run for a further 100 yr; by the end of this time the populations of trees had in all cases fallen to the very low levels sustained by the scattered available cells of 'Unfavourable A'. Such rapid declines are comparable to those seen in the pollen record from Lago Grande di Monticchio (Fig. 4) where tree pollen abundance values frequently fall sharply from peak to trough in only ca. 250 yr.

4. DISCUSSION

The simulations performed using MIGRATE allow us to reach a number of conclusions with respect to the hypothesis advanced by McGlone (1988), as well as to the more general issues of the extent to which the nature of the refugial populations of a tree during unfavourable periods may influence the form and rapidity of its response to a rapid change toward favourable conditions, and of how this response then may be recorded in the palæoecological record. The principal conclusions that emerge are as follows:

1 - The number and distribution of the refugial populations of a tree potentially may lead it to exhibit differences in the rapidity and sychronicity of its response to a rapid environmental change. However, the extent to which this will occur and/or be revealed by the palæoecological record depends upon two further factors:

a) Two trees with potential migration rates of the same magnitude may differ markedly in fecundity and dispersal characteristics. A tree of high fecundity but limited long-distance dispersal will expand rapidly across the landscape from numerous scattered refuges, exhibiting little or no lag; however, it will have a relatively shallow migration front when expanding from a discrete refuge so that it will exhibit a lag in its arrival relative to the environmental change, this lag increasing systematically with distance from its refuge.

A tree of lower fecundity but whose propagules achieve much greater long-distance dispersal will exhibit less rapid population expansion from numerous scattered refuges, its phase of most rapid expansion perhaps lagging markedly behind the environmental change to which it is a response. On the other hand it will have a relatively deep migration front and will rapidly appear at low density throughout the landscape even when expanding from a discrete refuge, its phase of most rapid population increase in consequence exhibiting a similar lag to that for expansion from numerous discrete populations.

Of the two, therefore, only the taxon with relatively high fecundity and a shallow migration front has the potential to exhibit markedly different patterns of population spread across a landscape of the inherent scale of the Italian peninsula or the islands of New Zealand according to the form of its initial distribution. What limited evidence there is of the depth of the migration fronts of trees expanding across Europe or eastern North America during the Holocene (Davis *et al.*, 1991) suggests that the Case I parameters, with their migration front depth of ca. 15 km, are closer to the typical situation. Thus we can predict that a majority of trees will have combinations of fecundity and dispersal characteristics that enable the form of their distribution under unfavourable conditions to be deduced from the palynological record of their response to a change to generally favourable conditions.

b) The radius of the pollen catchment of lakes of different size will, provided that the larger lakes examined have pollen catchments substantially larger in diameter than the depth of the migration front of the tree in question, influence the way in which different patterns of expansion are recorded in the palaeoecological record. The rapidity of the recorded expansion will not differ between larger and smaller lakes if it is from numerous scattered refugia, but will be reduced progressively in the records from larger lakes if it takes the form of migration from a distant refuge. Furthermore, only expansion from numerous scattered refugia can provide the most rapid increases, achieved within the space of a few generations of trees, in the records from larger lakes.

2 - The form of the refugial distribution of a tree taxon will determine its capacity to exhibit any regional response to a short-term environmental fluctuation. Only a taxon occupying numerous scattered refugia is likely to be able to exhibit such a regional response, and then only if it has the high fecundity required to sustain a relatively shallow migration front. A taxon with a migration front with a depth of a few tens of kilometres may exhibit a landscape-scale response to such an environmental fluctuation within as little as 5 generations.

3 - Over a wide range of possible values, the proportion of available habitat in the landcsape has a barely detectable effect upon the rapidity of the response of a taxon to a rapid environmental change.

In conclusion, our simulations support the hypothesis advanced by McGlone to account for the regionally rapid increase of tree taxa in New Zealand during deglaciation. It furthermore seems probable that the form of 'refugial' distribution that he hypothesised for New Zealand applied also to Chile (Markgraf & Kenny, 1996) and to southern Italy (Watts *et al.*, 1996a) during the last glacial; the rapidity of the expansion of tree taxa in both regions cannot otherwise readily be accounted for. Our results also provide the basis for a critical palæoecological test of the hypothesis; this would require an examination of the rapidity of the increase in pollen abundance, and hence in the tree population, of a taxon in the records from a series of lakes of markedly different sizes, and hence pollen catchments, within the same region. Only if the initial distribution of the tree was in numerous scattered small populations would it achieve a similar rate of increase in the pollen catchments of lakes of markedly different sizes.

A less stringent test requires only the demonstration of extreme rapidity of response in the record from a larger lake; the simulations suggest that increase to maximum population in the pollen catchment of such a lake can be achieved in less than 5 generations only if the initial population was present in numerous scattered refuges, and if the taxon has a sufficiently high fecundity. Lago Grande di Monticchio is a relatively large lake and may be expected to have a large pollen catchment; with a radius of ca. 300 m the work of Prentice (1988) indicates that the pollen catchment radii from within which 70% of the pollen of various taxa would be recruited is of the order of tens of kilometres (he cites values ranging between 5 km for *Fagus* and 59 km for *Pinus*). Large increases in tree pollen abundance during the last glacial stage are on several occasions achieved in less than 200 yr, and sometimes even less than 100 yr; this strongly supports the hypothesis that trees were present during the intervening unfavourable stages in numerous scattered small refuges in locally favourable microhabitats throughout the region. The rapid decreases in tree pollen abundance at Lago Grande di Monticchio also are matched by our simulations, showing that a tree population also can be rapidly reduced and constrained to such scattered favourable microhabitats within the landscape and thus providing an overall simulation that closely matches the fluctuations in tree populations recorded at this site (Watts *et al.*, 1996a) and in Chile (Markgraf & Kenny, 1996). Although such an hypothesis of the manner in which mesic trees survived glacial conditions in the mountainous regions of southern Europe has been discussed by previous authors, our simulations provide for the first time a means critically to assess this hypothesis.

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