



Estimated migration rates under scenarios of global climate change

Jay R. Malcolm^{1*}, Adam Markham^{2,4}, Ronald P. Neilson³ and Michael Garaci^{1,5} ¹*Faculty of Forestry, University of Toronto, Toronto, ON, Canada*, ²*World Wildlife Fund, Washington DC, USA*, ³*USDA Forest Service, Corvallis, OR, USA*, ⁴*Present address: Clean Air-Cool Planet, 100 Market Street, Suite 204, Portsmouth, NH 03801, USA* and ⁵*Present address: 32 Mulgrove Drive, Toronto, ON, Canada M9C 2R2*

Abstract

Aim Greenhouse-induced warming and resulting shifts in climatic zones may exceed the migration capabilities of some species. We used fourteen combinations of General Circulation Models (GCMs) and Global Vegetation Models (GVMs) to investigate possible migration rates required under CO₂-doubled climatic forcing.

Location Global.

Methods Migration distances were calculated between grid cells of future biome type *x* and nearest same-biome-type cells in the current climate. In 'base-case' calculations, we assumed that 2 × CO₂ climate forcing would occur in 100 years, we used ten biome types and we measured migration distances as straight-line distances ignoring water barriers and human development. In sensitivity analyses, we investigated different time periods of 2 × CO₂ climate forcing, more narrowly defined biomes and barriers because of water bodies and human development.

Results In the base-case calculations, average migration rates varied significantly according to the GVM used (BIOME3 vs. MAPSS), the age of the GCM (older- vs. newer-generation GCMs), and whether or not GCMs included sulphate cooling or CO₂ fertilization effects. However, high migration rates (≥ 1000 m year⁻¹) were relatively common in all models, consisting on average of 17% grid cells for BIOME3 and 21% for MAPSS. Migration rates were much higher in boreal and temperate biomes than in tropical biomes. Doubling of the time period of 2 × CO₂ forcing reduced these areas of high migration rates to c. 12% of grid cells for both BIOME3 and MAPSS. However, to obtain migration rates in the Boreal biome that were similar in magnitude to those observed for spruce when it followed the retreating North American Glacier, a radical increase in the period of warming was required, from 100 to > 1000 years. A reduction in biome area by an order of magnitude increased migration rates by one to three orders of magnitude, depending on the GVM. Large water bodies and human development had regionally important effects in increasing migration rates.

Main conclusions In conclusion, evidence from coupled GCMs and GVMs suggests that global warming may require migration rates much faster than those observed during post-glacial times and hence has the potential to reduce biodiversity by selecting for highly mobile and opportunistic species. Several poorly understood factors that are expected to influence the magnitude of any such reduction are discussed, including intrinsic migrational capabilities, barriers to migration, the role of outlier populations in increasing migration rates, the role of climate in setting range limits and variation in species range sizes.

Keywords

Global warming, plant migration, biomes, greenhouse effect, biodiversity.

*Correspondence: Faculty of Forestry, University of Toronto, Toronto, ON, Canada M5S 3B3. E-mail: jay.malcolm@utoronto.ca

INTRODUCTION

Directional climate change has resulted historically in significant shifts in the distributions of species and ecosystems (Davis, 1986). Shifts of tree distributions during the climatic warming of the recent glacial retreat are perhaps the best documented example, with species migrating at average rates of hundreds of metres per year or more for thousands of years (Huntley & Birks, 1983; Ritchie & Macdonald, 1986; Delcourt & Delcourt, 1987; King & Herstrom, 1997). Such directional climate change has the potential to affect biological communities in a profound manner. Because species vary fundamentally in the magnitude and timing of their responses, community composition may only partly reflect biotic processes such as predation and competition (Davis, 1986; Huntley & Webb, 1989). In fact, the role of migration and dispersal in structuring biological communities may be more pervasive than is generally appreciated. Clark *et al.* (1998) found that even in present-day closed canopy temperate forests, recruitment limitation because of low seed availability was true for many relatively common tree taxa and concluded that dispersal limitation at the within-stand level was likely to be an important factor affecting forest diversity and species composition (see also Matlack, 1994; Hubbell *et al.*, 1999).

In the next 100 years, greenhouse warming is projected to result in higher mean global temperatures than at any time in the past several million years (Crowley, 1990). As in the past, this climate change can be expected to lead to shifts in the geographical distributions of organisms. Perhaps equally significantly, however, the warming is expected to occur at a higher rate than during the glacial retreat, with potentially serious implications for biological communities (Davis & Zabinski, 1992). For example, Dyer (1995) used the spatial structure of modern landscapes to examine greenhouse-induced migration under wind and bird dispersal and concluded that even in a low disturbance landscape, migration rates fell short of projected global warming range shifts by at least an order of magnitude. Other studies have similarly concluded that plant migration could lag behind climatic warming, resulting in disequilibria between climate and species distributions, enhanced susceptibility of communities to natural and anthropogenic disturbances and eventual reductions in species diversity (Davis, 1989; Huntley, 1991; Overpeck *et al.*, 1991). A mismatch between the rate of warming and species migration could importantly influence ecosystem properties and processes, especially if tree populations are involved. In a scenario in which trees were perfectly able to keep up with warming, Solomon & Kirilenko (1997) found that $2 \times \text{CO}_2$ climate forcing resulted in a 7–11% increase in global forest carbon, whereas with no colonization of new sites, a 3–4% decline in forest carbon was observed. Kirilenko & Solomon (1998) used mean and maximum past tree migration rates to model transient vegetation responses and observed that large portions of the earth became occupied by unique and depauperate assemblages of plant functional types. Similarly,

using a detailed forest succession model for a site in southern Sweden, Sykes & Prentice (1996) found that compared with perfect migration, zero migration resulted in communities with fewer tree species, lower forest biomass and increased abundance of early successional species.

Unfortunately, despite the potential importance of plant migration in influencing ecosystem composition and functioning, migrational capabilities of species are poorly understood. Several models have assumed that trees would migrate at post-glacial rates (e.g. Kirilenko & Solomon, 1998); however, they may be able to move more quickly (Clark, 1998; Clark *et al.*, 1998). Even the relatively rapid migration rates of the past have proven difficult to explain; for example, it appears necessary to invoke infrequent long-distance dispersal events that are inherently difficult to quantify (Clark, 1998; see also Collingham *et al.*, 1996). In the light of this uncertainty, instead of asking how fast species and biomes might be able to move, we invert the problem in this paper and ask: how fast might species and biomes be required to move? Davis (1989) used the same approach in providing a simple metric of required change; namely, that temperature isolines were expected to move 100 km for every 1 °C of warming. Here, we undertake a more detailed analysis of possible future migration rates by comparing scenarios of current and future ($2 \times \text{CO}_2$ forcing) biome distributions provided by coupled General Circulation Models (GCMs) and Global Vegetation Models (GVMs). Instead of tracking migration rates along a single isoline (for example, along the northern limit of a biome or along a temperature isopleth), we calculated migration rates throughout the range of a biome, including areas where current and future distributions overlapped and hence required migration rates were zero. In addition, by using biome distributions to calculate migration rates, we implicitly focused on the more ecologically relevant derived climate variables used by the GVMs, rather than the raw climate data provided by the GCMs. We anticipate that the biome migration rates will provide information relevant to species migration rates. In some cases, species distributions are strongly associated with particular biome types. In addition, because the modelled biome distributions make use of variables that are directly relevant to plant physiology, at least in a heuristic sense the distributions can be viewed as proxies for climatically determined species distributions. Of course, species distributions are often smaller or larger than biome distributions, and perhaps more importantly, species may occur in only a fraction of their climatically possible range. Therefore, we investigated these factors indirectly by examining the importance of the breadth of biome definitions in influencing future migration rates.

Our specific objectives were to: (1) compare required migration rates among a range of coupled GCMs and GVMs (fourteen combinations in total), (2) test the importance of inherent differences among the models in influencing migration rates (including the age of the GCM, the presence or absence of sulphate cooling, the GVM used and direct CO_2 effects on plant water use efficiency), (3) investigate global variation in migration rates; for example, as a function of

biome type and latitude and (4) undertake sensitivity analyses of key assumptions in the migration rate calculations; namely, the time period to attain $2 \times \text{CO}_2$ forcing, the breadth of biome definitions and the role of impediments to migration such as large water bodies and anthropogenic development.

METHODS

Climate scenarios and global vegetation models

A standardized series of GCMs and GVMs such as that used in VEMAP (VEMAP Members, 1995) was not available at the global scale; however, fourteen combinations of models were available to us. These included seven GCMs and two GVMs. The latter were run in some cases, both with and without direct physiological CO_2 effects. Neilson *et al.* (1998) used a similar set of model combinations to investigate global changes in biome area, leaf area index and runoff.

The GCMs consisted of four older equilibrium GCM scenarios and three newer transient simulations. We include the older runs for comparative purposes and because most published analyses have relied on them. The older GCMs were relatively simple mixed-layer ocean-atmosphere models used to simulate equilibrium climate under $2 \times \text{CO}_2$ forcing and included GISS, GFDL-R30, OSU and UKMO (IPCC, 1990). The transient GCMs made use of coupled atmospheric-ocean dynamics and in one case included sulphate aerosol forcing. They consisted of two from the Hadley Centre [HADCM2GHG (no sulphate) and HADCM2SUL (with sulphate)] and one from the Max Planck Institute (MPI) for Meteorology (Neilson *et al.*, 1998; see also Giorgi *et al.*, 1998). The course grids of the GCMs were interpolated to 0.5-degree latitude/longitude grids. Climate change scenarios were created by applying ratios and differences from $1 \times \text{CO}_2$ and $2 \times \text{CO}_2$ simulations back to a baseline monthly climate data set (see Neilson *et al.*, 1998). To calculate future climate from the transient GCMs, a 30-year (Hadley Centre) or 10-year (Max Planck Institute) climate average was extracted from the current period (e.g. 1961–90) and the period approximating $2 \times \text{CO}_2$ forcing (e.g. 2070–99).

The two GVMs were BIOME3 (Haxeltine & Prentice, 1996) and MAPSS (Neilson, 1995). These models made use of ecological and hydrological processes and plant physiological properties to simulate the equilibrium distribution of potential vegetation on upland, well-drained sites under average seasonal climate conditions. A simulated mixture of generalized life forms such as trees, shrubs and grasses that can coexist at a site is assembled into a vegetation type classification (Neilson *et al.*, 1998). MAPSS and BIOME2 (a precursor to BIOME3) produced generally similar results for the coterminous United States. However, compared with BIOME2, MAPSS was consistently more sensitive to water stress, producing more xeric future outcomes and had a larger benefit from CO_2 -induced increased water-use efficiency (VEMAP Members, 1995).

MAPSS and BIOME3 were run under the two Hadley Centre scenarios, whereas only BIOME3 was run under the MPI scenario and only MAPSS was run under the GFDL, GISS, OSU and UKMO scenarios. GVMs that made use of the Hadley Centre and MPI climate were run both with and without direct CO_2 effects, whereas in keeping with the VEMAP analyses, the older climate change scenarios were run only with direct CO_2 effects (Neilson *et al.*, 1998).

Overall patterns of biome change

To compare major patterns of biome change among models, we used principal components analysis (PCA). Indirectly, this analysis also provided information on migration rates because models with similar distributions of biome change can be expected to exhibit similar migration rates. To create a grid of biome change for each GCM/GVM combination, we compared results from the $2 \times \text{CO}_2$ climate run scenario against the corresponding current-climate run and scored cells that underwent biome change as '1' and those that underwent no change as '0.' The resulting grid of cell change for each model combination was transformed to a vector by concatenating grid rows. The resulting fourteen vectors, which had 259,200 grid cells each, were concatenated to create a $259,200 \times 14$ matrix (in standard multivariate parlance, the 259,200 rows were 'observations' and the fourteen columns were 'variables'). Vectors with relatively similar patterns of zeros and ones will have similar eigenvectors in the PCA. Therefore, to assess overall patterns of variability among models, we plotted eigenvector scores.

Calculations of migration rates

We calculated migration rates under a single set of assumptions (termed 'base-case' calculations) to investigate influences of GCM/GVM combination, geographical location and biome type. Differences among the GCM/GVM combinations were compared statistically by calculating the overall mean migration rate for each combination and then conducting parametric tests on the means. Thus, in these tests the unit of replication was the model combination. To improve normality and homogeneity of variances (as indicated in plots of residuals), prior to calculating the means, migration rates were log transformed [$\log_{10}(\text{migration rate} + 1)$]. Differences investigated were: GVM type, GCM age, presence or absence of sulphate cooling and direct effects of CO_2 on plant water use efficiency. Where possible, we held the GCM or GVM type constant to reduce extraneous variation. For example, we could investigate both the importance of GVM type and sulphate cooling for just Hadley Centre runs. Note that these tests are based on only a small subset of available GCMs and GVMs and hence should be taken as indicative rather than conclusive.

In addition to the base-case calculations, we varied three assumptions that we expected to influence migration rates; namely, the time period of climate forcing, the breadth of biome definitions and the method used to calculate migration rates.

Time period of climate change

The time period of $2 \times \text{CO}_2$ climate forcing is the divisor in migration rate calculations and hence importantly influences required migration rates. Based on IPCC estimates, in base-case calculations we assumed 100 years. This assumption is based on a mid-range emission scenario of doubling of CO_2 in 70 years (IS92a) and *c.* 30-year lag in the temperature response as envisaged under 'medium' (2.5 °C) climate sensitivity (IPCC, 1990; IPCC, 1992). Note that because of the coarse grid resolution, the smallest non-zero migration rate at the equator was 550 m year^{-1} (i.e. 0.5° of latitude or longitude in 100 years). Thus, low non-zero migration rates were restricted to high latitudes.

For comparison, we used a more conservative time period, namely 200 years. Additionally, we took advantage of research on post-glacial rates of spruce (*Picea* A. Dietr.) migration undertaken by King & Herstrom (Fig. 7 in Clark *et al.*, 1998) and compared *Picea* rates against migration rates in the Boreal biome. We used the Boreal biome because the current geographical distribution of *Picea* in North America is fairly well approximated by the Boreal biome. In the analysis, we varied the time period of forcing until we achieved maximum agreement between the Boreal and *Picea* rates.

Number of vegetation types

In general, narrowly defined climate envelopes can be expected to exhibit higher average migration rates than more broadly defined ones because as envelopes decrease in size, their average migration rates will increasingly approximate the migration rates of envelope boundaries themselves. The implication is that, all else being equal, species with smaller climatically determined ranges will need to attain higher migration rates than species with larger climatically determined ranges. Following Neilson *et al.* (1998), in the base-case calculations we used ten biome types (see Table 1). In another set of calculations, we used the original GVM-specific number of biome types (eighteen for BIOME3 and forty-five for MAPSS). We also investigated the relationship between migration rate and biome area by plotting mean migration rate against biome area for biomes in North America and Africa (HADCM2SUL only, without increased water use efficiency). The area of a grid cell was calculated as $\cos(\text{latitude})$ multiplied by 3066 km^2 (the approximate area of a 0.5 by 0.5° grid cell at the equator). To calculate mean migration rates, the migration rates of cells were weighted by the corresponding cell area. Because biomes in Africa tended to be distributed into northerly and southerly portions, we calculated biome rates and areas separately for biomes north and south of the equator. This made the African biomes more contiguous and hence more comparable with the North American biomes. Biomes with fewer than twenty grid cells were excluded from the plots.

Migration distances

We reasoned that the nearest possible immigration source for a grid cell of future biome type *x* would be the nearest grid cell of the same biome type in the current climate. Thus, migration distance was calculated as the distance between a

future cell and its nearest same-biome-type cell in the climate. In base-case calculations, we used 'crowfly' distances; that is, the shortest distances between cell centres. However, these crowfly distances ignored potential barriers to migration such as bodies of water. To take this into account, additionally we made use of Dijkstra's algorithm (Winston, 1994) to calculate 'shortest terrestrial' distances, which consisted of the shortest summed distances between linking centres of neighbouring terrestrial cells (including diagonally linked cells). Thus, shortest paths were calculated avoiding water bodies. In both methods, distances between cell centres were calculated using software from the States National Oceanic and Atmospheric Administration (FORTRAN subroutine INVER1, written by L. Pfister and modified by J. G. Gergen) using the 1984 World Geodetic System reference ellipsoid.

In addition to water barriers, we investigated the impact of anthropogenic habitat loss on migration rates by removing from the shortest path calculations cells that were 'highly impacted' by human activities. These highly impacted cells were assumed to be completely impermeable to migration; that is, in the shortest path calculations they behaved as though they were water. Our definition of 'highly impacted' was based on model results by Turner (referred to as Pitelka *et al.*, 1997) which suggested that three-quarters of movement although fragmented landscapes occurs within approximately 55% or 85% of habitat was lost (depending on whether fragmentation was random or aggregated, respectively). Simulations by Schwartz *et al.* (1997) also indicated shifts in migration rates at close proximity to human activities (depending on whether dispersal followed exponential or inverse power functions, respectively). To quantify habitat destruction, we made use of the global unsupervised classification of AVHRR satellite data taken by the United States Geological Service (Lambert *et al.*, 2000). We classified 0.5 -degree cells as 'highly impacted' if 55% or 85% of the underlying 1-km^2 cells were human modified [i.e. their Olson global land use type designations contained the words 'crop', 'fire', 'flooded', 'town' or 'urban' (17 of the 94 types)].

RESULTS

Overall patterns of biome change

In the principal component analysis on biome change, the percentage variance explained dropped off markedly after the first two eigenvalues (38% and 23%, respectively for the first two vs. 8% and 7% for the next two). Therefore, we plotted only the first two eigenvectors. Interestingly, the variation from the fourteen GCM/GVM combinations was more important in determining patterns of cell change than variation among GCMs. In the light of the large difference between the two first eigenvectors, we present results from the two GVMs separately. In agreement with VEMAP (VEMAP 1995), the effect of increased water use efficiency

Table 1 Vegetation types in two Global Vegetation Models and their assignment to ten biome types used in the 'base-case' migration rate calculations

Base-case	BIOME3	MAPSS
1. Tundra	Arctic/alpine tundra Polar desert	Tundra Ice
2. Taiga/Tundra	Boreal deciduous forest/woodland	Taiga/Tundra
3. Boreal Conifer Forest	Boreal evergreen forest/woodland	Forest Evergreen Needle Taiga
4. Temperate Evergreen Forest	Temperate/boreal mixed forest	Forest Mixed Warm Forest Evergreen Needle Maritime Forest Evergreen Needle Continental
5. Temperate Mixed Forest	Temperate conifer forest Temperate deciduous forest	Forest Deciduous Broadleaf Forest Mixed Warm Forest Mixed Cool Forest Hardwood Cool Forest Evergreen Broadleaf Tropical
6. Tropical Broadleaf Forest	Tropical seasonal forest Tropical rain forest	Forest Seasonal Tropical Forest Savanna Dry Tropical
7. Savanna/Woodland	Temperate broad-leaved evergreen forest Tropical deciduous forest Moist savannas Tall grassland Xeric woodlands/scrub	Tree Savanna Deciduous Broadleaf Tree Savanna Mixed Warm Tree Savanna Mixed Cool Tree Savanna Mixed Warm Tree Savanna Evergreen Needle Maritime Tree Savanna Evergreen Needle Continental Tree Savanna PJ Continental Tree Savanna PJ Maritime Tree Savanna PJ Xeric Continental Chaparral Open Shrubland No Grass Broadleaf Shrub Savanna Mixed Warm Shrub Savanna Mixed Cool Shrub Savanna Evergreen Micro Shrub Savanna SubTropical Mixed Shrubland SubTropical Xeromorphic Shrubland SubTropical Mediterranean Shrubland Temperate Conifer Shrubland Temperate Xeromorphic Conifer
8. Shrub/Woodland	Short grassland	Grass Semi-desert C3 Grass Semi-desert C3/C4 Grassland Semi Desert Grass Northern Mixed Tall C3 Grass Prairie Tall C4 Grass Northern Mixed Mid C3 Grass Southern Mixed Mid C4 Grass Dry Mixed Short C3 Grass Prairie Short C4 Grass Northern Tall C3 Grass Northern Mid C3 Grass Dry Short C3 Grass Tall C3 Grass Mid C3 Grass Short C3 Grass Tall C3/C4 Grass Mid C3/C4 Grass Short C3/C4 Grass Tall C4 Grass Mid C4 Grass Short C4
9. Grassland	Dry savannas Arid shrubland/steppe	Shrub Savanna Tropical Shrub Savanna Mixed Warm Grass Semi-desert C4
10. Arid Lands	Desert	

Table 1 continued

Base-case	BIOME3	MAPSS
		Desert Boreal
		Desert Temperate
		Desert Subtropical
		Desert Tropical
		Desert Extreme

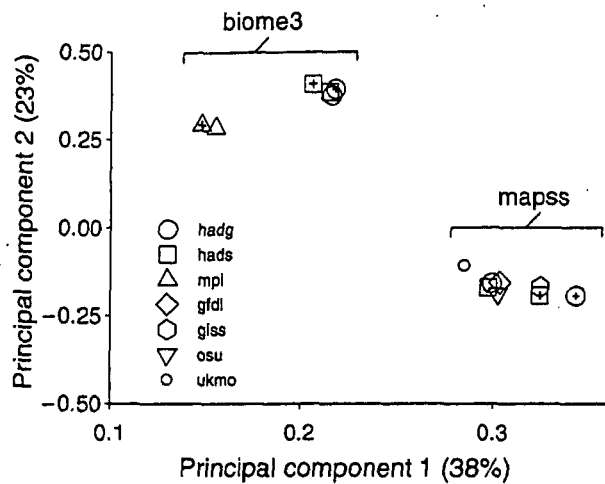


Figure 1 Eigenvector scores from a Principal Components Analysis on biome change between current and CO₂-doubled climate conditions as modelled by fourteen combinations of General Circulation and Global Vegetation Models. For HADG (no sulphate cooling), HADS (with sulphate cooling) and MPI, symbols with pluses indicate models with increased water use efficiency.

also differed between the two GVMs. For BIOME3, paired runs from the same GCM, but with different water use efficiency, were nearly superimposed. In contrast, paired MAPSS runs nearly spanned the entire range of model results for MAPSS, indicating greater sensitivity to CO₂ fertilization effects. Among BIOME3 runs, two groupings were evident: the Max Planck Institute runs (with and without WUE) and the four Hadley Centre runs (with and without WUE and with and without aerosol cooling). Among MAPSS models, results from the older GCMs overlapped broadly with those from the newer Hadley Centre runs.

Base-case migration rates

Comparisons of mean migration rates confirmed the important influence of GVM type. Mean log-transformed migration rates averaged significantly lower for BIOME3 than for MAPSS [respective means [$\log_{10}(\text{migration rate} + 1)$] were 0.93 (SD = 0.10, $n = 6$) and 1.26 (SD = 0.18, $n = 8$); $F_{1,12} = 16.07$, $P = 0.002$]. Across the fourteen model combinations, BIOME3 consistently had more cells with low migration rates (< 316 m year⁻¹) than MAPSS, comprising

on average 71% of cells vs. 61% for BIOME3 (Fig. 2). [Note that because of coarse grid resolution, and hence the paucity of low non-zero migration rates, > 97.5% of the grid cells in the < 316 m year⁻¹ class had rates equal to zero (as averaged across the fourteen model combinations)]. Conversely, BIOME3 had consistently fewer cells than MAPSS in the 316–999 m year⁻¹ class, and although not always consistent among GCMs, fewer in the 1000–9999 m year⁻¹ class. Although average migration rates differed significantly between the two GVMs, both showed similar patterns in that ‘very high’ migration rates (≥ 1000 m year⁻¹) were relatively common, comprising on average 17% of cells for BIOME3 and 21% for MAPSS. Migration rates of $\geq 10,000$ m year⁻¹ were rare (< 1% of cells for each model).

Although relatively minor compared to differences between the two GVMs, differences among the GCMs also significantly influenced migration rates. Among MAPSS runs, older GCMs had significantly higher log-transformed migration rates than the newer GCMs [respective means were 1.38 (SD = 0.18, $n = 4$) and 1.14 (SD = 0.06, $n = 4$); $F_{1,6} = 5.99$, $P = 0.05$]. A two-way ANOVA comparing Hadley Centre results according to GVM and presence/absence of sulphate cooling indicated not only that BIOME3 had lower rates on average than MAPSS [respective log-transformed mean rates were 0.88 (SD = 0.11, $n = 2$) and 1.15

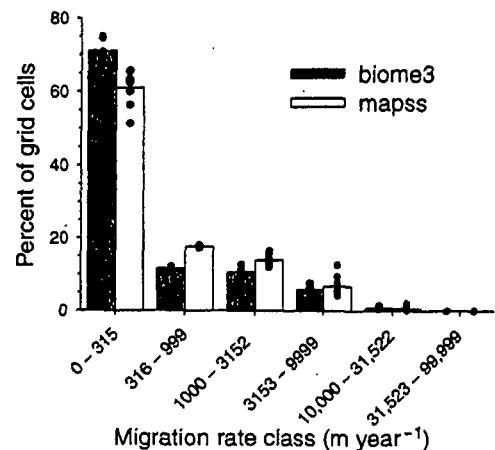


Figure 2 Average percentage of grid cells in various migration rate classes for two Global Vegetation Models. Dots represent individual Global Circulation Models.

(SD = 0.08, $n = 2$); ANOVA $F_{1,1} = 236.94$, $P = 0.04$], but also that models with sulphate cooling had slightly lower average migration rates than the models without cooling [respective log-transformed mean rates were 0.95 (SD = 0.20, $n = 2$) and 1.08 (SD = 0.18, $n = 2$); ANOVA $F_{1,1} = 58.05$, $P = 0.08$]. For BIOME3, incorporation of increased water use efficiency through direct CO₂ effects led to consistently and significantly higher log-transformed migration rates (mean difference between pair-specific averages [efficiency minus no efficiency] was 0.15, paired- $t = 8.41$, $P = 0.01$, $n = 3$). The same was not true for MAPSS (mean difference between pair averages [efficiency minus no efficiency] was -0.01, paired- $t = -0.57$, $P = 0.67$, $n = 2$).

To visually examine spatial variation in migration rates, for each grid cell we calculated the percentage of model combinations that exhibited relatively high (≥ 1000 m year⁻¹) migration rates. We used 1000 m year⁻¹ as a cut-off point because tree migration rates in the palaeorecord were usually below this (Clark, 1998). High migration rates that were relatively consistent among models (i.e. $\geq 50\%$ of models) were common in the northern hemisphere and included large areas in Canada, Alaska, Russia and Fennoscandia (Fig. 3). Other areas with consistently high

rates included parts of eastern Brazil, Uruguay, eastern Argentina, the savanna/rainforest border in Africa, southern England, Saudi Arabia, Iraq, central India, north-eastern China, Thailand, Cambodia and Australia. Distinct banding paralleling the orientation of biome boundaries was evident in several areas, including Canada, Africa, and northern Asia. These bands reflected the high migration rates required to track the leading edges of pole-ward-shifting biomes.

The high migration rates in the northern hemisphere also were evident when migration rates were compared among latitudinal classes. Lowest migration rates were observed within 20° of the equator, where 6–8% (BIOME) or 11–13% (MAPSS) of grid cells had migration rates ≥ 1000 m year⁻¹ (Fig. 4). Average migration rates were nearly constant up to 40° of latitude for BIOME3, but thereafter jumped markedly. The highest migration average was in the northernmost latitudinal class ($> 60^\circ$), where 35% of cells had rates ≥ 1000 m year⁻¹. The relationship between latitudinal class and average migration rate was more monotonic for MAPSS. However, maximum migration rates were again observed in the northernmost latitudinal class and were similar in magnitude to those observed for BIOME3.

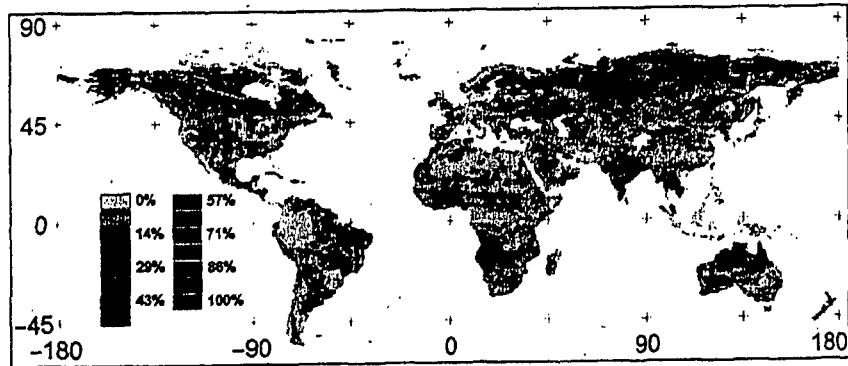


Figure 3 Percentage of fourteen combinations of General Circulation and Global Vegetation Models that showed migration rates ≥ 1000 m year⁻¹.

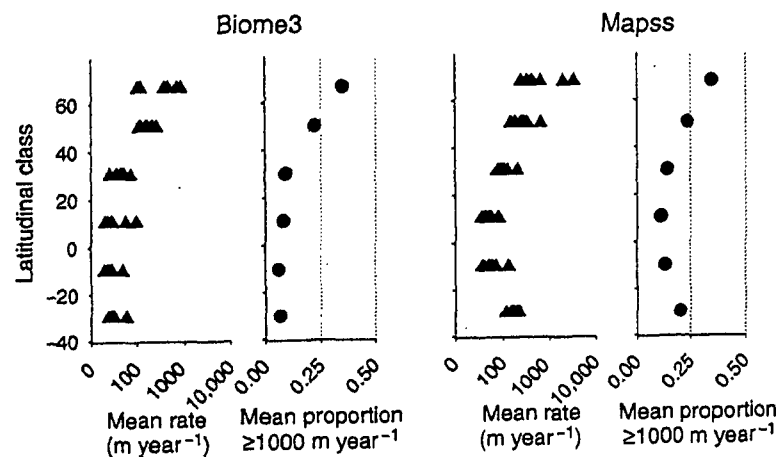


Figure 4 Mean migration rates and proportions of grid cells with rates ≥ 1000 m year⁻¹ for 20-degree latitudinal classes. Positions on the ordinate represent the mean latitudes of the cells within the classes.

Not surprisingly given this variation according to latitude, average migration rates for both GVMs were markedly higher in biomes found at high latitudes (Taiga/Tundra, Temperate Evergreen Forest, Temperate Mixed Forest and Boreal Coniferous Forest) than elsewhere (Fig. 5). In these high-latitude biomes, on average approximately 35% of cells had rates $\geq 1000 \text{ m year}^{-1}$, with a maximum of 44% in Temperate Mixed Forest (MAPSS) and a minimum of 27% for Temperate Evergreen Forest (MAPSS). Average migration rates in the other biome types (excluding Tundra) tended to be higher for MAPSS (on average, 13% of cells $\geq 1000 \text{ m year}^{-1}$) than for BIOME3 (9%). Because Tundra, in general, did not shift to new areas, but instead was encroached upon, it had average migration rates close to zero in both GVMs.

The time period of climate change

Doubling the period of $2 \times \text{CO}_2$ forcing from 100 to 200 years decreased the percentage of cells with very high migration rates ($\geq 1000 \text{ m year}^{-1}$) by about one-third for BIOME3 (17.4 to 11.8%) and by nearly one half for MAPSS (21.3 to 11.9%) (Table 2). A doubling of the warming period, however, did little to bring Boreal migration rates into agreement with *Picea* rates observed during the glacial

retreat. A best fit between Boreal and *Picea* rates was obtained when the period of warming was instead increased by approximately an order of magnitude, to 1070 years for BIOME3 and to 1150 years for MAPSS (Fig. 6a). At these best-fit values, an average of only 1.3% of non-zero Boreal cells had rates $\geq 1000 \text{ m year}^{-1}$ (Fig. 6c). For 100-year warming on the other hand, percentages of non-zero Boreal cells equalling or exceeding 1000 m year^{-1} averaged 61% for both BIOME3 and MAPSS (Fig. 6b). The time period of warming appeared in the denominator of the migration rate calculations, hence the curves in Fig. 6a followed the curvilinear form expected for an inverse function. From these curves, a slight increase in the time period of the warming had a disproportionate effect in reducing migration rates.

Number of biome types

As expected, more narrowly defined biomes yielded higher average migration rates. Compared with base-case calculations (ten biome types), eighteen biome types for BIOME3 and forty-five for MAPSS yielded, respectively, 10% and 14% more grid cells above 316 m year^{-1} . This increase in migration rates was confirmed in a plot of average migration rate against biome area for Africa and

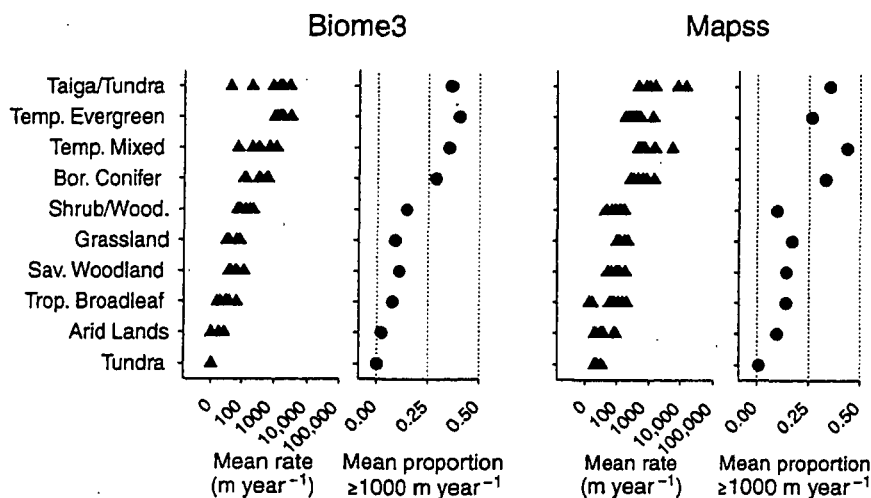


Figure 5 As Fig. 4, except that rates and proportions are shown for ten biome types.

Table 2 Mean (\pm SEM) percentage of grid cells in six migration rate classes for two Global Vegetation Models and for two time periods of $2 \times \text{CO}_2$ climate forcing. Sample size (n) is the number of General Circulation Models

Migration rate class (m year^{-1})	BIOME3 ($n = 6$)		MAPSS ($n = 8$)	
	100-year warming	200-year warming	100-year warming	200-year warming
0–315	71.1 \pm 1.23	79.6 \pm 1.11	61.0 \pm 1.75	73.7 \pm 1.86
316–999	11.6 \pm 0.26	9.6 \pm 0.45	17.7 \pm 0.10	14.4 \pm 0.33
1000–3152	10.6 \pm 0.53	8.8 \pm 0.52	13.9 \pm 0.57	9.3 \pm 0.87
3153–9999	5.9 \pm 0.57	1.9 \pm 0.43	6.6 \pm 1.05	2.5 \pm 0.66
10,000–31,522	0.9 \pm 0.18	0.1 \pm 0.03	0.6 \pm 0.22	0.09 \pm 0.04
31,523–99,999	0.03 \pm 0.008	0.01 \pm 0.006	0.03 \pm 0.02	0.004 \pm 0.0005

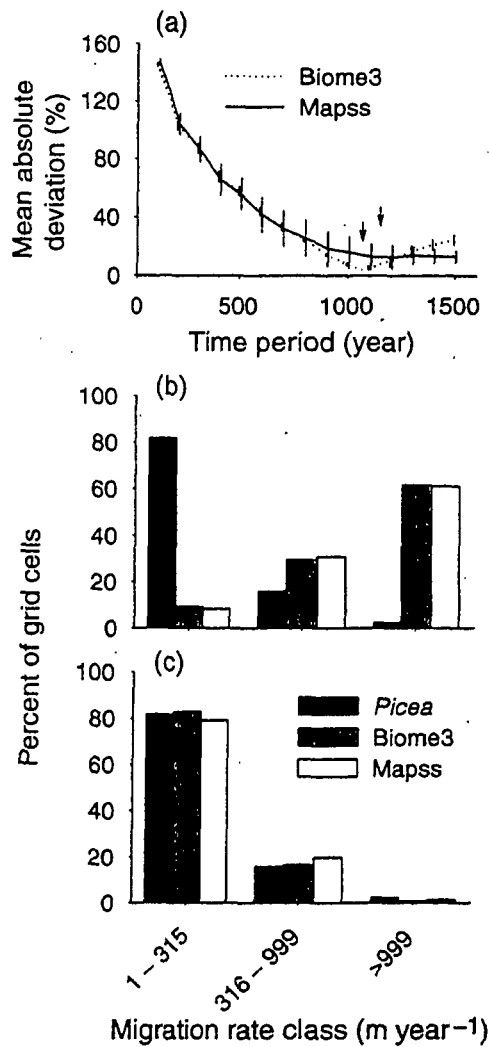


Figure 6 (a) Average (\pm SEM) migration rates of cells in the boreal biome as a function of the time period of $2 \times \text{CO}_2$ forcing. Holocene estimates for *Picea A. Dietr.* are compared with migration rates calculated (b) assuming 100-year forcing or (c) 'best-fit' forcing. The 'best fit' values (1070 years for BIOME3 and 1150 years for MAPSS, as shown by the arrows) were those that minimized deviations between the heights of histogram bars (as quantified by the sum of the absolute values of the deviations).

North America (Fig. 7). Based on the fitted regression lines, as biome area decreased by an order of magnitude, average BIOME3 migration rates increased by approximately an order of magnitude and average MAPSS rates by nearly three orders of magnitude. The importance of latitude in influencing migration rates was evident in that for a given biome area, North American regression lines were above African ones. After transforming back to non-logged values, Y-intercepts of linear regressions were 45 m year^{-1} for North America and 5 m year^{-1} for Africa for BIOME3 and, respectively, 110 and 31 m year^{-1} for MAPSS.

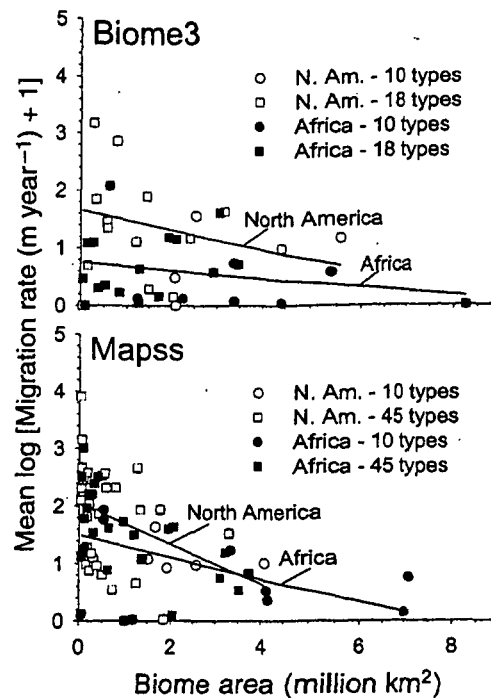


Figure 7 Mean log-transformed migration rate plotted against biome area for biomes in North America and Africa. Calculations are for two Global Vegetation Models (BIOME3 and MAPSS) and one General Circulation Model (HADCM2SUL). For each Global Vegetation Model, results for two global biome classification schemes are shown: ten biomes and the original number of biomes used in the model (eighteen for BIOME3; forty-five for MAPSS). African biome migration rates and areas were calculated separately for biomes north and south of the equator.

Crowfly vs. shortest-path distances

Migration rates calculated using crowfly and shortest-terrestrial-path distances were usually similar. Averaged across all models, 99% of grid cells had shortest-path rates that were within 316 m/year of their crowfly rates (99.1 and 98.9 for BIOME3 and MAPSS, respectively; see Table 3). The exceptions tended to be on islands (such as Newfoundland) and peninsulas (such as western Finland) (Fig. 8).

Respectively, 20.0% and 11.7% of terrestrial cells were 55% or 85% 'human modified.' When these cells were rendered off limits to migration, shortest-path migration rates changed only slightly. Compared with shortest-terrestrial-path distances, the percentage of cells that changed their migration rates by $< 316 \text{ m year}^{-1}$ averaged between 97% and 99% for the two GVMs (Table 3). Cells with large increases in migration rates ($\geq 1000 \text{ m year}^{-1}$) tended to be concentrated along the northern edges of developed areas in the northern temperate and boreal zone, especially in north-western Russia, Finland, central Russia and central Canada (Fig. 9).

Table 3 Mean (\pm SEM) percentage of grid cells in various classes of migration rate increase for 'shortest-path' distance calculations relative to the 'crowfly' distances and for two habitat loss scenarios relative to shortest-path calculations

Increase in migration rate (m year ⁻¹)	Shortest-path		Shortest-path plus 55% habitat loss		Shortest-path plus 85% habitat loss	
	BIOME3 (n = 6)	MAPSS (n = 8)	BIOME3 (n = 6)	MAPSS (n = 8)	BIOME3 (n = 6)	MAPSS (n = 8)
0–315	99.1 \pm 0.075	98.9 \pm 0.181	97.6 \pm 0.346	97.0 \pm 0.288	99.1 \pm 0.146	98.0 \pm 0.176
316–999	0.65 \pm 0.055	0.63 \pm 0.084	1.32 \pm 0.199	1.06 \pm 0.092	0.53 \pm 0.072	0.90 \pm 0.059
1000–3152	0.12 \pm 0.025	0.21 \pm 0.046	0.50 \pm 0.075	0.74 \pm 0.107	0.25 \pm 0.049	0.76 \pm 0.102
3153–9999	0.05 \pm 0.002	0.13 \pm 0.028	0.28 \pm 0.083	0.82 \pm 0.073	0.13 \pm 0.029	0.17 \pm 0.008
10,000–31,522	0.02 \pm 0.002	0.08 \pm 0.011	0.08 \pm 0.016	0.06 \pm 0.010	0.01 \pm 0.002	0.01 \pm 0.002
31,523–99,999	0	0.001 \pm 0.0005	0.002	0	0	0
Undefined*	0.08 \pm 0.016	0.041 \pm 0.005	0.19 \pm 0.022	0.30 \pm 0.025	0.08 \pm 0.008	0.13 \pm 0.016

*Cells for which there was no path to a $1 \times \text{CO}_2$ cell of the same biome type.

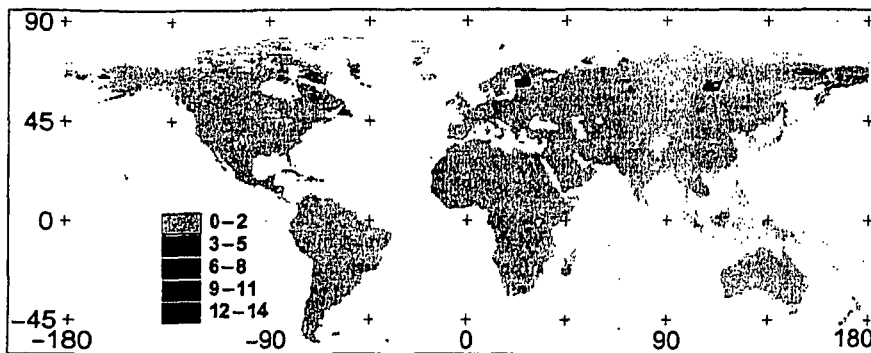


Figure 8 Number of models for which migration rates calculated using shortest terrestrial path distances were more than 1000 m year⁻¹ greater than migration rates calculated using crowfly distances.

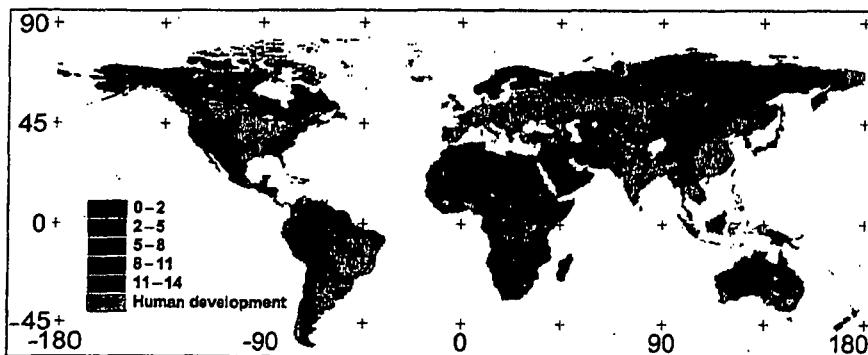


Figure 9 Number of models for which migration rates calculated from shortest terrestrial path distances excluding human modified habitat were more than 1000 m year⁻¹ greater than migration rates calculated using all terrestrial cells. Map cells were judged to be human modified if 55% of the cell was composed of anthropogenic habitat (see text for details).

DISCUSSION

Several of the differences inherent among the GCMs and GVMs significantly influenced biome migration rates. Sulphate cooling and lower water use efficiency of plants resulted in lower rates (the latter only for BIOME3, however), as did newer- vs. older-generation GCMs. Most important in influencing migration rates, however, was the GVM type, with MAPSS showing higher migration rates than BIOME3. The higher migration rates for MAPSS reflected greater vegetation type change, which presumably resulted from its greater sensitivity to water stress, a

characteristic that was noted in a comparison between MAPSS and BIOME2 (a precursor to BIOME3; VEMAP Members, 1995). This difference between the models, as well as others [such as different sensitivities to direct CO_2 effects and different regional accuracies in mapping vegetation types (VEMAP Members, 1995; Neilson *et al.*, 1998)] indicate that considerable uncertainties exist with respect to the realistic modelling of potential vegetation distributions.

Despite this variation among models, however, all models agreed that under $2 \times \text{CO}_2$ forcing, large areas of the globe had rates ≥ 1000 m year⁻¹ (Fig. 3). Thus, although the scenarios cannot be viewed as predictive (VEMAP

Members, 1995), the wide range of assumptions about $2 \times \text{CO}_2$ climate forcing and vegetation responses in the different models all indicated the potential for high required migration rates and suggest that the migration estimates are robust. For example, in the base-case calculations (100-year $2 \times \text{CO}_2$ forcing, crowfly distances, and ten biome types), an average of 17% of terrestrial grid cells had rates $\geq 1000 \text{ m year}^{-1}$ for BIOME3 and 21% for MAPSS. Such high rates were rarely observed in the palaeorecord (Ritchie & Macdonald, 1986; Delcourt & Delcourt, 1987; King & Herstrom, 1997; Clark, 1998; Wilkinson, 1998), suggesting that global warming has the potential to impose substantially higher migration rates than during post-glacial times. Indeed, in our comparison of post-glacial *Picea* migration rates and required rates in the boreal biome, 100-year forcing revealed required rates approximately an order of magnitude higher than the post-glacial rates, in general agreement with Dyer (1995) and Iverson & Prasad (1998). High required rates were especially common for high latitude biomes (excluding tundra), where an average of 27–44% of grid cells had rates above 1000 m year^{-1} . These higher migration rates in temperate areas are expected because of the greater rates of warming envisioned for higher latitudes (IPCC, 1996). Even in tropical biomes, however, considerable vegetation change was projected by the models, resulting in approximately one grid cell in ten (9–13%) having migration rates $\geq 1000 \text{ m year}^{-1}$.

From a biodiversity perspective, a critical issue is the ability of organisms to keep pace with these required rates. Just as global warming may incur a local 'extinction debt' in that warming of a certain magnitude may impose future extinctions as some species eventually disappear in response to the unsuitable climatic conditions (see Tilman *et al.*, 1994), it may also incur a 'migration deficit' in that other species may fail to arrive to take advantage of the newly appropriate climatic conditions. Here, we define migration deficit as the difference between the number of species that have arrived at a locality and the number that would be expected if the warming rate was within migration capabilities. This potential filtering effect with respect to migrational capabilities is analogous to that observed during agricultural development, when a premium on long-range dispersal results in the selection of a recognizable 'old-field' flora pre-adapted to human disturbance (Matlack, 1994). Global warming may therefore be another factor resulting in a 'weedier' future of more highly mobile, opportunistic and climatically tolerant species (Bazzaz, 1996; Sykes & Prentice, 1996; Walker & Steffen, 1997).

Unfortunately, migrational capabilities of species are poorly known. Even for temperate trees, whose migrational capabilities are among the best studied, capabilities are poorly understood. Temperate trees were apparently able to closely track the climate changes that accompanied the glacial retreat (Prentice *et al.*, 1991); however, maximum intrinsic rates are unknown. Even the high post-glacial rates are difficult to explain (Collingham *et al.*, 1996; Clark, 1998).

As a result, the magnitude of any migration deficit imposed by a mismatch between the rate of climate envelope

shifts and species migrational capabilities is highly uncertain. At present, it appears safe to conclude that whereas some organisms will be able to keep up with these shifts, others will not. For invasive species and others with high dispersal capabilities, migration rates exceeding 1000 m year^{-1} may be common. For example, Weber (1998, Fig. 4) found that range diameters of two goldenrod (*Soldago* L.) species invading Europe increased from 400 to 1400 km between 1850 and 1875 and from 1400 to 1800 km between 1875 and 1990. Assuming a circular range expanding evenly outward, respective migration rates are approximately 20,000 and 1740 m year^{-1} . Similarly, after its arrival in western North America in about 1880, cheatgrass (*Bromus tectorum* L.) had occupied most of its range of 200,000 km² in approximately 40 years (Mack, 1986). Again assuming a circular range expansion, a 40-year period to traverse the radius gives a migration rate of 6300 m year^{-1} . An example of high migrational capabilities for an animal is provided by the coyote (*Canis latrans* Say), which migrated at $> 20,000 \text{ m year}^{-1}$ from the region south and west of lake Michigan in 1900 to arrive in Newfoundland by 1990 [see Figs 2 and 3 in Parker (1995)].

Invasive species may be atypical of other plants and animals because of their often abnormally high fecundity and dispersal capabilities and because their dispersal is often human-aided. Possible examples of species with slow migration rates come from studies of re-invasions of forest herbs into previously plowed secondary forests. Both Matlack (1994) and Brunet & Von Oheimb (1998) found that distance from old-growth correlated with understory richness in the secondary forests, suggesting migration limitation. Matlack (1994) found no measurable movement for some species and only four of fifty-one showed rates as high as $2\text{--}3 \text{ m year}^{-1}$. Similarly, Brunet & Oheimb (1998) reported a median migration rate of only 0.3 m year^{-1} for forty-nine species. Among animals, earthworms may provide an example of an animal species with low migration capabilities and a possible filtering effect of glaciation, having not yet re-invaded most of the areas from which they were extirpated during glaciation (Reynold, 1977; Gates, 1982; Lee, 1985). Where they do occur in that area, they are introduced European species (Gates, 1982). Experimentation also supports low migrational capabilities for earthworms; for example, an established *Allolobophora* Eisen species invaded limed and fertilizer pastures in New Zealand at 10 m year^{-1} (Stockdill, 1982) and in a reclaimed polder in Netherlands, two *Allolobophora* species spread at rates of 6 and 4 m year^{-1} (Van Rhee, 1969). Hoogerkamp *et al.* (1983) estimated that after an initial lag of 1–2 years, migration rates of five species were *c.* $4.5\text{--}9 \text{ m year}^{-1}$. The filtering effect that glaciation imposed for earthworms may also be true of some plant species (e.g. Arroyo *et al.*, 1996). If so, our results suggest even greater filtering for global warming. High required migration rates in tropical areas are of particular concern given the potential contribution of long-term climatic stability to high species diversity in these areas (Richards, 1996) and the possibility of lower intrinsic rates of migration than in the temperate and boreal zones.

The lack of understanding of migrational capabilities appears to be further compounded by possible differences between post-glacial and present-day site conditions. Brunet & Von Oheimb (1998) pointed out that although the understory flora that they studied appeared to be migrating very slowly, it had evidently migrated into southern Sweden from remote refugia during the last glaciation and therefore had shown much higher migration rates in the past. They suggested that compared with past migration, contemporary migration was limited by such factors as seed predation, availability of suitable microsites and vigour of clonal growth. Presumably, the newly opened colonization sites exposed by the glacier presented a very different environment for migrating species in comparison with today's already established communities (Dyer, 1995). In the absence of significant disturbance, many plant communities are quite resistant to invasion and community-level changes may be delayed for many decades (Pitelka *et al.*, 1997). For example, forest communities modelled by Davis & Botkin (1985) showed 100–200 years time-lags in the replacement of dominant species although seedlings were available for all species throughout the experiment. For prairie communities, higher diversity appears to decrease susceptibility to invasion (Tilman, 1997, 1999; Knops *et al.*, 1999). Migration rates observed under modern conditions therefore may better reflect capabilities under global warming than higher post-glacial rates. Alternatively, the disturbance created by global warming itself may increase possibilities for migration and hence contribute to increased migration rates.

Any filtering effect of global warming is of concern not only because of potential impoverishment of communities, but also because of possible secondary changes in ecosystem function. Migration of co-evolved taxa, for example, would presumably be limited by migration rates of the slowest moving species. Although animals can often migrate more quickly than plants, in many cases their habitat depends on suitable plant communities. Trees are of particular concern because of their dominant roles in modulating resource availability ['ecosystem engineers' *sensu* Lawton & Jones (1995)]. If tree migration is limiting, one could expect large changes in ecosystem composition and function (e.g. Sykes & Prentice, 1996; Solomon & Kirilenko, 1997; Kirilenko & Solomon, 1998) which may have cascading effects on animal communities. Changes in overstorey tree communities as a result of global warming – including forest die-back, transitions from forested to non-forested ecosystems or domination by early successional taxa – can all be expected to result in widespread changes in forest species composition and global geochemical cycling.

The time period of climatic forcing

As noted by Kirilenko & Solomon (1998), rapid climate change can be expected to widen the gap between suitable climatic conditions for a species and the establishment locations permitted by slow migration. Our comparisons of Boreal and *Picea* migration rates suggested that a reduction in the rate of global warming approximately by an order

magnitude would be required to bring future rates in line with the rapid ecological change observed over the course of the glacial retreat. However, our results also provide a more encouraging result for policy. As indicated by the concave upward shape of the curve in Fig. 6a, relatively large reductions in required migration rates can be obtained by relatively modest increases in the time period of $2 \times \text{CO}_2$ forcing. A doubling of the time period of $2 \times \text{CO}_2$ forcing from 100 to 200 years led to a substantial decrease in the global area subjected to high migration rates and had a larger effect in ameliorating migration rates than subsequent 100-year increments.

Geographical range sizes

Several potentially important factors influencing migration rates were excluded from the present analysis. First, because of rapid in-filling between populations, outlier populations may lead to more rapid migration than that along a single population front (Davis *et al.*, 1991; Pitelka *et al.*, 1997; Clark, 1998). As noted by Davis (1986), plants continue to compete tenaciously for space even in the face of changed conditions and, as evidenced by glacial refugia (e.g. Abbot *et al.*, 2000), relictual populations can survive for many years. Many organisms can maintain at least regional representation for long time periods even in the face of unfavourable conditions. Although trees and perennials are at a disadvantage with respect to rapidly shifting climate envelopes because of slow maturity and low reproductive rates (Pitelka *et al.*, 1997), these same factors may promote the maintenance of outlier populations that can serve as sources of colonists. Secondly, the analysis suffers from the exclusive use of climate variables to define distributional boundaries. Numerous factors other than climate are important in determining species distributions (e.g. Davis *et al.*, 1998a,b). If a species occurs in only a subset of its possible climatic range, but climate is nonetheless used to model its actual distribution, then estimated climate-induced migration distances will be erroneously high.

Both of the above factors argue for the use of relatively liberal estimates of range sizes in estimating climatically induced migration rates. As expected, we found that as biome distribution sizes decreased, required migration rates increased, albeit not strikingly across the range of sizes that we investigated. The use of biome distributions as proxies for species climate envelopes, even in a heuristic sense, must therefore be treated with caution. Even within a taxonomic group, the relationship between average biome area and average range size shows considerable variation. For example, for common US tree species east of the 100th meridian, even our coarsest (ten-type) biome classification underestimated average range sizes. From Iverson *et al.* (1999), seventy-five tree taxa mapped by Little (1971, 1977) [cited in Iverson *et al.* (1995)] had average range sizes of 1.59 million km², which was larger than the average ten-class biome sizes for the same region (0.67 million km² for both BIOME3 and MAPSS). By contrast, for 819 species in the genus *Eucalyptus* L'Herit in Australia, average range size

was 0.11 million km² (Hughes *et al.*, 1996). This was smaller than the average areas of our narrowest biome definitions in the same region [0.85 million km² for BIOME3 (eighteen biome types) and 0.45 million km² for MAPSS (forty-five biome types)].

Finally, important additional limitations of the analysis here include failures to consider the full spectrum of possible CO₂ fertilization effects (Bazzaz *et al.*, 1996) and possible effects of population density on migration. Concerning the latter, Schwartz's (1992) simulations showed that rare species never attained their highest migration rates even when suitable habitat was abundant. This is an important concern for many plant species; for example, the Nature Conservancy estimates that one-half of endangered plant taxa in the US are restricted to five or fewer populations (from Pitelka *et al.*, 1997).

Barriers to migration

Not surprisingly, incorporation of large water bodies as migration barriers led to substantially higher required migration rates on islands and peninsulas, just as exclusion of anthropogenically modified habitats led to higher migration rates along the poleward margins of developed areas. Neither effect was widespread, although both were sometimes regionally important. For example, both factors contributed to higher migration rates in Finland than in neighbouring regions. Schwartz (1992) concluded that species migrations might be channelled around areas of development; a corollary is that migration might be especially limiting along the margins of developed areas. Our results support the possibility that appropriate management within developed areas could improve prospects for migration (Peters & Darling, 1985). The analysis presented here, however, is approximate in several respects. Migration across water or developed habitat was treated as an all-or-none process. Of course, the width of a barrier will affect the probability of traversing it. For example, there is little evidence of any lag in post-glacial migration because of Finland's peninsular nature (C. Prentice, Pers. comm.). Our analysis also made use of large grid cells, meaning that only relatively extensively developed areas were excluded from migration and that diffusion processes present at small spatial scales were lost (Dyer, 1995). The use of the USGS classification also led to a strong focus on agricultural development; other less intensive forms of development were ignored. For example, Schwartz (1992) noted that compared with the original primary forest, the uneven quality of secondary forests of the north-eastern US could influence colonization by slow-growing shade tolerant trees and exacerbate differences in migration rates among species.

In conclusion, evidence from coupled GCMs and GVMs suggests that global warming may require migration rates much faster than those observed during post-glacial times. These rates have the potential to reduce local biodiversity as species fail to keep pace with shifting climatic conditions. A full consideration of biodiversity impacts must consider not

only migration, but also the abilities of existing populations to persist in the face of changed climatic conditions. Unfortunately, migrational capabilities are poorly known, and it does not appear possible at present to quantify the magnitude of the global warming induced migration deficit. Increases in connectivity among natural habitats within developed landscapes may help organisms to attain their maximum intrinsic rates of migration. Although substantial decreases in the rate of warming appear necessary to bring future rates in line with rates observed during the glacial retreat, relatively modest decreases in the rate of warming may result in substantial decreases in future migration rates.

ACKNOWLEDGMENTS

Funding was from World Wildlife Fund and the Natural Sciences and Engineering Research Council of Canada. We would like to thank Dave Martell, who provided computer time for the shortest-path calculations and C. Prentice, J. Ray, S. Thomas, and an anonymous reviewer, who made helpful comments on an earlier draft of the manuscript. S. James provided references on earthworm movements.

REFERENCES

- Abbott, R.J., Smith, L.C., Milne, R.I., Crawford, R.M.M., Wolff, K. & Balfour, J. (2000) Molecular analysis of plant migration and refugia in the Arctic. *Science*, 289, 1343–1346.
- Arroyo, M.T.K., Riveros, M., Peñaloza, A.P., Cavieres, L.C. & Faggi, A.M.F. (1996) Phytogeographic relationships and regional richness patterns of the cool temperate rainforest flora of southern South America. *High-latitude rainforests and associated ecosystems of the West Coast of the Americas: climate, hydrology, ecology, and conservation* (eds R.G. Lawford, P.B. Alaback and E. Fuentes), pp. 134–172. Springer, New York.
- Bazzaz, F.A. (1996) *Plants in changing environments: linking physiological, population, and community ecology*. Cambridge University Press, Cambridge.
- Bazzaz, F.A., Bassow, S.L., Berntson, G.M. & Thomas, S.C. (1996) Elevated CO₂ and terrestrial vegetation: implications for and beyond the global carbon budget. *Global change and terrestrial ecosystems* (eds B. Walker and W. Steffen), pp. 43–76. Cambridge University Press, Cambridge.
- Brunet, J. & von Oheimb, G. (1998) Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology*, 86, 429–438.
- Clark, J.S. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist*, 152, 204–224.
- Clark, J.S., Fastie, C., Hurr, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb, T. & Wyckoff, P. (1998) Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *Bioscience*, 48, 13–24.
- Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, 68, 213–235.

- Collingham, Y.C., Hill, M.O. & Huntley, B. (1996) The migration of sessile organisms: a simulation model with measurable parameters. *Journal of Vegetation Science*, **7**, 831–846.
- Crowley, T.J. (1990) Are there any satisfactory geologic analogs for a future greenhouse warming? *Journal of Climate*, **3**, 1282–1292.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998a) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S. (1998b) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology*, **67**, 600–612.
- Davis, M.B. (1986) Climatic instability, time lags, and community disequilibrium. *Community ecology* (eds J. Diamond and T.J. Case), pp. 269–284. Harper & Row, New York.
- Davis, M.B. (1989) Lags in vegetation response to greenhouse warming. *Climatic Change*, **15**, 75–82.
- Davis, M.B. & Botkin, D.B. (1985) Sensitivity of cool temperate forests and their fossil pollen record to rapid temperature change. *Quaternary Research*, **23**, 327–340.
- Davis, M.B., Schwartz, M.W. & Woods, K. (1991) Detecting a species limit from pollen in sediments. *Journal of Biogeography*, **18**, 653–668.
- Davis, M.B. & Zabinski, C. (1992) Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. *Global warming and biology diversity* (eds R.L. Peters and T.E. Lovejoy), pp. 297–308. Yale University Press, New Haven, CT, USA.
- Delcourt, P.A. & Delcourt, H.R. (1987) *Long-term forest dynamics of the temperate zone: a case study of late-quaternary forests in eastern North America*, 439 p. Springer-Verlag, New York.
- Dyer, J.M. (1995) Assessment of climatic warming using a model of forest species migration. *Ecological Modelling*, **79**, 199–219.
- Gates, G.E. (1982) Farewell to North American megadriales. *Megadriologica*, **4**, 12–77.
- Giorgi, F., Meehl, G.A., Kattenberg, A., Grassl, H., Mitchell, J.F.B., Stouffer, R.J., Tokioka, T., Weaver, A.J. & Wigley, T.M.L. (1998) Simulation of regional climate change with global coupled climate models and regional modeling techniques. *The regional impacts of climate change: an assessment of vulnerability* (eds R.T. Watson, M.C. Zinyowera, R.H. Moss and D.J. Dokken), pp. 429–437. Cambridge University Press, Cambridge.
- Haxeltine, A. & Prentice, I.C. (1996) BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochemical Cycles*, **10**, 693–709.
- Hoogerkamp, M., Rogaar, H. & Eijsackers, H.J.P. (1983) Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. *Earthworm ecology: from Darwin to vermiculture* (ed. J.E. Satchell), pp. 85–105. Chapman & Hall, New York.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & de Lao, S.L. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science*, **283**, 554–557.
- Hughes, L., Cawsey, E.M. & Westoby, M. (1996) Geographic and climatic range sizes of Australian eucalypts and a test of Rapoport's rule. *Global Ecology and Biogeography*, **5**, 128–142.
- Huntley, B. (1991) How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany*, **67** (Suppl. 1), 15–22.
- Huntley, B. & Birks, H.J.B. (1983) *An atlas of past and present pollen maps of Europe: 0–13,000 Years Ago*, p. 667. Cambridge University Press, Cambridge.
- Huntley, B. & Webb, T. III (1989) Migration: species' response to climatic variations caused by changes in the earth's orbit. *Journal of Biogeography*, **16**, 5–19.
- IPCC (1990) *Climate change: the IPCC scientific assessment* (eds J.T. Houghton, G.J. Jenkins and J.J. Ephraums), Cambridge University Press, Cambridge.
- IPCC (1992) *Climate change 1992: the supplementary report to the IPCC scientific assessment* (eds J.T. Houghton, B.A. Callander and S.K. Varney). Cambridge University Press, Cambridge.
- IPCC (1996) *Climate change 1995: the science of climate change* (eds J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg and K. Maskell), p. 572. Cambridge University Press, Cambridge.
- Iverson, L.R. & Prasad, A.M. (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*, **68**, 465–485.
- Iverson, L.R., Prasad, A.M., Hale, B.J. & Sutherland, E.K. (1999) *Atlas of current and potential future distributions of common trees of the eastern United States*, p. 245. United States Department of Agriculture, Forest Service, Northeastern Research Station (General Technical Report NE-265), Radnor, PA, USA.
- King, G.A. & Herstrom, A.A. (1997) Holocene tree migration rates objectively determined from fossil pollen data. *Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota* (eds B. Huntley, W. Cramer, A.V. Morgan, H.C. Prentice and J.R.M. Allen), pp. 91–101. Springer, Berlin.
- Kirilenko, A.P. & Solomon, A.M. (1998) Modeling dynamic vegetation response to rapid climate change using bioclimatic classification. *Climatic Change*, **38**, 15–49.
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Groth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecological Letters*, **2**, 286–293.
- Lawton, J.H. & Jones, C.G. (1995) Linking species and ecosystems: organisms as ecosystem engineers. *Linking species and ecosystems* (eds C.G. Jones and J.H. Lawton), pp. 141–150. Chapman & Hall, New York.
- Lee, K.E. (1985) *Earthworms: their ecology and relationships with soils and land use*, p. 411. Academic Press, Sydney.
- Loveland, T.R., Reed, B.C., Brown, J.F., Ohlen, D.O., Zhu, Z., Yang, L. & Merchant, J.W. (2000) Development of a global land cover characteristics database and IGBP DISCover from 1 km AVHRR data. *International Journal of Remote Sensing*, **21**, 1303–1330.

- Mack, R.N. (1986) Alien plant invasion in to the intermountain west: a case history. *Ecology of biology invasions of North America and Hawaii* (eds H.A. Mooney and J.A. Drake), pp. 191–212. Springer-Verlag, New York.
- Matlack, G.R. (1994) Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology*, **75**, 1491–1502.
- Neilson, R.P. (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications*, **5**, 362–385.
- Neilson, R.P., Prentice, I.C., Smith, B., Kittel, T. & Viner, D. (1998) Simulated changes in vegetation distribution under global warming. *The regional impacts of climate change: an assessment of vulnerability* (eds R.T. Watson, M.C. Zinyowera, R.H. Moss and D.J. Dokken), pp. 441–456. Cambridge University Press, Cambridge.
- Overpeck, J.T., Bartlein, P.J. & Webb, T. III (1991) Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science*, **254**, 692–695.
- Parker, G. (1995) *Eastern coyote: the story of its success*, p. 254. Nimbus Publishing, Halifax, Canada.
- Peters, R.L. & Darling, J.D.S. (1985) The greenhouse effect and nature reserves. *BioScience*, **35**, 707–717.
- Pitelka, L.F., Ash, J., Bradshaw, R.H.W., Berry, S., Brubaker, S., Clark, S., Davis, M.B., Dyer, M., Gardner, R.H., Gitay, H., Hengeveld, R., Hope, G., Huntley, B., James, L., James, S., King, G.A., Lavorel, S., Mack, R.N., Malanson, G.P., McGlone, M., Noble, I.R., Prentice, I.C., Rejmanek, M., Saunders, A. & Sykes, M. (1997) Plant migration and climate change. *American Scientist*, **85**, 464–473.
- Prentice, I.C., Bartlein, P.J. & Webb, T. III (1991) Vegetation and climate changes in eastern North America since the last glacial maximum. *Ecology*, **72**, 2038–2056.
- Reynolds, J.W. (1977) The Earthworms of Massachusetts (Oligochaeta: Lumbricidae, Megascolecidae and Sparganophilidae). *Megadriologica*, **3**, 49–54.
- Richards, P.W. (1996) *The tropical rain forest: an ecological study*, 2nd edn, p. 575. Cambridge University Press, Cambridge.
- Ritchie, J.C. & MacDonald, G.M. (1986) The patterns of post-glacial spread of white spruce. *Journal of Biogeography*, **13**, 527–540.
- Schwartz, M.W. (1992) Modelling effects of habitat fragmentation on the ability of trees to respond to climatic warming. *Biodiversity and Conservation*, **2**, 51–61.
- Solomon, A.M. & Kirilenko, A.P. (1997) Climate change and terrestrial biomes: what if trees do not migrate? *Global Ecology and Biogeography*, **6**, 139–148.
- Stockdill, S.M.J. (1982) Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia*, **24**, 29–35.
- Sykes, M.T. & Prentice, I.C. (1996) Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. *Climatic Change*, **34**, 161–177.
- Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81–92.
- Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455–1474.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.
- Van Rhee, J.A. (1969) Development of earthworm populations in polder soils. *Pedobiologia*, **9**, 128–132.
- VEMAP Members (27 authors) (1995) Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles*, **9**, 407–437.
- Walker, B. & Steffen, W. (1997) An overview of the implications of global change for natural and managed terrestrial ecosystems. *Conservation Ecology (Online)*, **1**, 2.
- Weber, E. (1998) The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography*, **25**, 147–154.
- Wilkinson, D.M. (1998) Mycorrhizal fungi and Quaternary plant migrations. *Global Ecology and Biogeography*, **7**, 137–140.
- Winston, W.L. (1994) *Operations research: applications and algorithms*, 3rd edn, p. 1318 (+54). Duxbury Press, Belmont, CA, USA.

BIOSKETCHES

In addition to climate change research undertaken in collaboration with a variety of national and international organizations, Jay Malcolm has studied community and landscape ecology in Amazonia, central Africa, and central Ontario.

Adam Markham directs Clean Air-Cool Planet, a New Hampshire-based non-profit organization promoting solutions to climate change in the Northeast. Previously, he directed World Wildlife Fund's international climate campaign and has written extensively on climate change and biodiversity issues.

Ron Neilson is a bioclimatologist with the USDA Forest Service and a Professor (Courtesy) with Oregon State University. His research focusses on factors limiting species distributions. The MAPSS model of vegetation distributions developed by his team has been used in a variety of IPCC and US government reports.

Michael Garaci obtained his Master of Science at the University of Toronto studying fluvial geomorphology. He is currently the GIS Project Coordinator at the Pressure Pipe Inspection Company in Mississauga, Ontario.