

# HOW WILL NEW ZEALAND'S FORESTS RESPOND TO CLIMATE CHANGE? POTENTIAL CHANGES IN RESPONSE TO INCREASING TEMPERATURE

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## ABSTRACT

If temperature increases occur during the next century as predicted by climatologists, then major changes in New Zealand's natural and plantation forests can be expected. Current relationships between temperature and occurrence of natural forest species suggest major changes in forest pattern with an increase in temperature. Because of widely varying relationships between species and climate, changes will likely occur at a species, rather than at a community level. Initial changes should favour species with wide tolerance to climatic factors, good dispersal capacity, and short generation times. Shifts in distribution will be influenced by the availability of sites for colonisation, i.e., they will depend on mortality of the current site occupants. Disruption in forest composition is most likely to occur in forest patches where there is little potential for dispersal of new, more suitable species. This could result from a narrow, within-patch temperature range, geographic isolation from other patches which might act as seed sources, or dependence on longer-distance latitudinal rather than shorter-distance altitudinal migration.

The plantation estate across the country can be classified in relation to present-day temperature and rainfall regimes. The mean annual temperature is between 10° and 15°C for 90%, and between 10° and 11°C for 35% of the plantation area. Mean annual rainfall is between 1250 and 2250 mm for 75% of the plantation area. If the worst-case climate change scenario is realised, then 96% of the plantation area will experience mean annual temperatures above 13°C. Twenty-one percent of the plantation area will experience mean annual temperatures above 17°C which is near the top of the optimal temperature range for growth of *Pinus radiata* D. Don, and warmer than any current values in the present climate. The effect of this on timber yield and log quality is still uncertain.

Recommendations for future research include an extension of the current analysis to a national scale for natural forests, and an urgent need for process studies to investigate the effects of climate variables, particularly temperature and carbon dioxide, on the physiological response of all forest species. This is required as a basis for further modelling of the long-term ecological effects.

**Keywords:** climate change; natural forest; plantation forest; species distribution; temperature; rainfall; bioclimatic analysis; *Pinus radiata*.

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## INTRODUCTION

It is generally agreed by climatologists that the global increase in mean temperature of 0.3° to 0.7°C during the last 100 years is consistent with the effects of an increase in greenhouse gases. Globally, the warmest years this century have occurred during the last decade (Jones *et al.* 1988) and the temperature in New Zealand is probably warmer now than it has been for several thousand years (Salinger 1988). If this trend continues, an increase in mean temperature up to 3.0° ± 1.5°C at New Zealand latitudes can be expected by the year 2050, with rather less certain changes in rainfall and changes in the frequency and severity of extreme climatic events (Salinger & Pittock 1991).

Natural forests in New Zealand occupy 6.2 million ha (22.9% of total land area) and plantation forests a further 1.3 million ha (4.6%) (Turland & Neumann 1991). The production forest is mainly *Pinus radiata* (89%), with the remainder mainly *Pseudotsuga menziesii* (Mirb.) Franco. Export earnings from forest products currently exceed \$1.4 billion per year (Ministry of Forestry 1991). Trees and tree crops are particularly vulnerable to climate change, since the time scale for the projected increase in temperature is short in relation to their lifespan. Because of the rapid nature of projected changes, there is little time for plantation tree genotypes better-suited to the future climate to be identified and established, and present genotypes may be unable to acclimate fast enough to the new climatic conditions. Our objective in this paper was to undertake an initial assessment of the likely impacts of climate change for forests in New Zealand, identifying resources which are particularly at risk and areas where further research is a high priority.

Although there has been little quantitative study of the relationships between natural forests and climate in New Zealand, elsewhere climate has been shown to be a major determinant of forest pattern at regional to global scales (e.g., Box 1981; Holdridge 1967; Walter 1979; Sowell 1985; Neilson 1987). Changes in forest distribution which occurred with the climatic amelioration following the last glacial period have also been well documented (e.g., Prentice 1986; Webb 1986; McGlone 1988). Despite the documented examples of relationships between climate and vegetation pattern at the landscape level, our lack of understanding of the mechanisms by which climate controls vegetation pattern (Woodward 1986) makes prediction of the impacts of future climatic change on natural communities difficult. Some progress can be made using techniques which correlate distribution of species with climate variables, e.g., Emmanuel *et al.* (1985) and the approach adopted in this paper.

Many of the problems apparent for natural forests are not applicable to plantation forests since they are artificially established, management is intensive, and competition between species can be controlled. For plantation forests, the emphasis is not on pattern but on survival of species, productivity, and wood quality. Results from physiological studies with *Pinus radiata* have enabled first-order estimates of climate change on plantations in New Zealand and Australia to be made (Barlow & Conroy 1988; Booth & McMurtrie 1988; Hollinger 1988, 1990), and have provided the parameters for biologically based models which allow simulation of forest productivity in relation to future climate (Booth & McMurtrie 1988). However, uncertainties in future climate projections, and lack of information on the response of trees to interacting effects of such variables as temperature, rainfall, carbon dioxide concentration, disease and pests, and weed competition, make any predictions

of future forest productivity speculative. The first step is to identify the areas of plantation forest which are particularly at risk.

## PROCEDURES

### Natural Forests

In the absence of detailed information on physiological responses of individual species to climate variables, we extended results from an earlier correlative analysis of the relationships between climate and distribution of major tree species in the central North Island region by Leathwick & Mitchell (1992). In that study, mathematical surfaces fitted to climate station data (Hutchinson 1988; Mitchell 1991) were used to derive estimates of annual mean temperature, annual rainfall, and solar radiation for approximately 1350 plots, each 0.4 ha. The other site variables recorded for each plot were depth of the Taupo pumice soil, and topography. Logistic regression equations (McCullagh & Nelder 1983) were used to derive the relationships between the presence of species, and the climate and other site variables. In this study we used the equations developed by Leathwick & Mitchell (1992) to calculate the probability of occurrence for selected species in relation to mean annual temperature. This was then used to predict the effects of an elevation in annual temperature of 1.5° or 3°C on the occurrence of the species. These increases in temperature were chosen to be consistent with “most likely scenario” and the “alternative warm scenario” for conditions in the period 2030 to 2050 (Royal Society of New Zealand 1988; Salinger & Pittock 1991). The other climatic and site variables for each plot were not changed.

### Plantation Forests

The statistical database for the plantation forest resource in New Zealand used in the analysis was from the National Exotic Forest Description at April 1988 (Novis *et al.* 1989). The database was compiled from returns supplied by all owners of forests with plantation areas exceeding 500 ha, and encompassed approximately 85% of the country's total forest resource, with statistics from the previous year being used to compile the residual.

The appropriate latitudes and longitudes were determined for each forest from a map (New Zealand Forest Service 1986). For each forest, long-term annual average rainfall and temperature data for the nearest meteorological station were taken from summaries of climatological observations to 1980 (New Zealand Meteorological Service 1983). No attempt was made to modify the climate variables for changes in topography within each forest. In a manner similar to that used for the natural forests, conditions of temperature and rainfall for the period 2030 to 2050 were calculated from climate change scenarios (Royal Society of New Zealand 1988; Salinger & Pittock 1991). Annual mean temperature and rainfall data for each forest were modified according to the “most likely scenario” and the “alternative warm scenario” for each region (Salinger & Hicks 1989). Depending on the region and the scenario, the limits of the predicted increase in temperature were between 1.4° and 3.5°C and the limits of the predicted change in annual rainfall were between -10% and 15%.

## RESULTS AND DISCUSSION

### Natural Forests

Response to temperature varied between species, i.e., different species occupy different parts of the total range of temperature found in the central North Island area studied (Fig. 1). The range of temperatures over which species are found also varies, e.g., *Beilschmiedia tawa* (A.Cunn.) Kirk (*tawa*) occurs over a range of only 3° to 4°C, but *Weinmannia racemosa* L.f. (*kamahahi*) and *Prumnopitys ferruginea* (D.Don) de Laub. (*miro*) occur over ranges greater than 6°C.

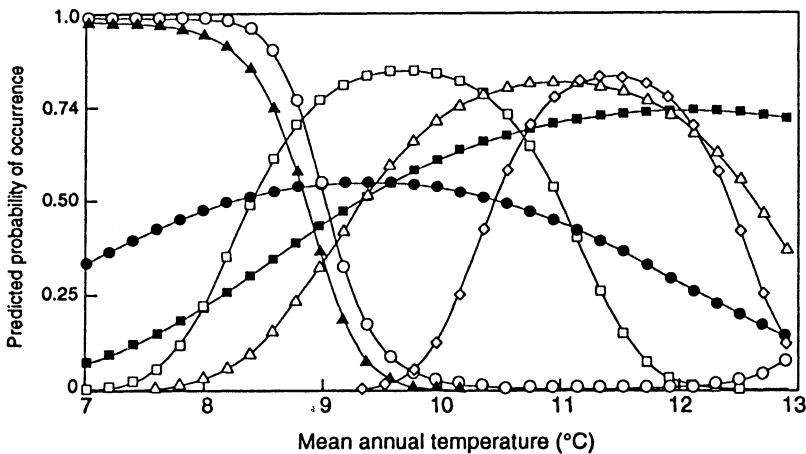


FIG. 1—Probabilities of occurrence of selected indigenous species in the central North Island in relation to temperature. Probabilities were calculated from regression equations fitted to presence/absence data from approximately 1350 plots, each 0.4 ha. Other variables were set at fixed values as follows: rainfall = 1500 mm, solar radiation = average, Taupo pumice depth = 0, topography = flat. The symbols refer to ■ *Weinmannia racemosa*, □ *Podocarpus spicatus*, ● *Prumnopitys ferruginea*, ○ *Nothofagus fusca*, ▲ *Nothofagus solandri var. cliffortioides*, Δ *Dacrydium cupressinum*, and ◇ *Beilschmiedia tawa*.

The degree of overlap between current and predicted future ranges for species will depend on the magnitude of the temperature shift, the terrain, and the range of temperatures over which they occur. Overlaps will be greatest for species with a wide temperature tolerance under conditions of small temperature increase and in areas with wide altitudinal variation. Under the more extreme climate change scenarios proposed for the region, i.e., a rise of the order of 3°C, species currently occurring over narrow temperature ranges (e.g., *B. tawa* in Fig. 1) can be expected to shift in time to new ranges with little overlap with their current distribution (Fig. 2).

The final magnitude of shifts in the distributions of species will depend on the availability of suitable sites at higher latitude and/or altitude, with suitable higher altitude sites adjacent to the current range reducing the distance required for migration. An example is illustrated in Fig. 2 where, as a result of a 3°C rise in temperature, there is a southwards shift in sites predicted to support *B. tawa* of approximately 1° in latitude, and an associated shift upwards in altitude of approximately 300 m.

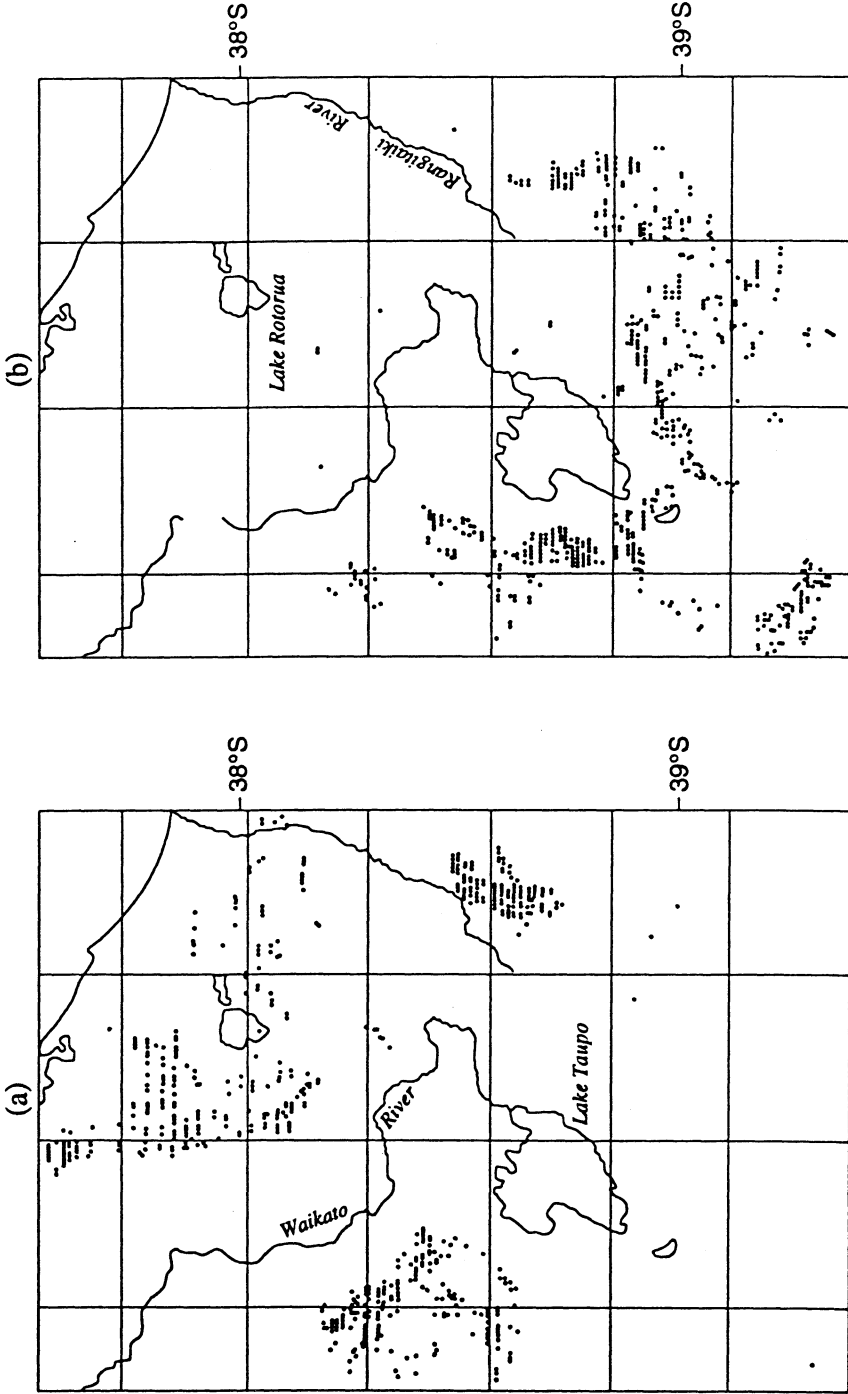


FIG. 2.—Predicted shift in the distribution of *Beilschmiedia tawa* in the central North Island with a rise in mean annual temperature of 3°C, (a) present-day distribution and (b) sites predicted to have greater than 50% chance of the species being present, following the rise in temperature. The grids on the map are 30 × 40 km and latitude is shown on the right-hand margin.

In the study by Leathwick & Mitchell (1992) temperature was shown to be the dominant climate factor determining pattern but other climate variables, e.g., solar radiation and rainfall, were also important for most species, as were interactions between the variables. The highly variable nature of these relationships suggests that species will respond to climate change in an individualistic fashion, rather than at a community level. Although some simple migration of existing combinations of species to higher latitudes or altitudes is possible, particularly for communities which are floristically simple, the development of communities formed from new combinations or proportions of species appears much more likely.

Because the geographic distribution of temperatures is a function of both latitude and altitude, shifts in distribution can be expected towards both higher latitudes and higher altitudes. The regression equations of Norton (1985) suggest that for each degree rise in temperature, species will need to shift either 2.22° southwards in latitude (approximately 250 km), or 200 m upwards in altitude to maintain their current position in relation to temperature.

Plant response times to climate change are likely to be highly variable, and will depend on the time required to reach maturity, seed dispersal capabilities, and availability of suitable sites for invasion (Woodward 1986). Responses will be fastest for generalist plants with good long-distance dispersal capacity and short generation times, i.e., little delay between establishment and production of new propagules, and slowest for site-specialised, long-lived trees, with poor dispersal capacity and long generation time. As a consequence, we predict that there will be a general shift in the composition of New Zealand's natural forests which will favour species with wide tolerance (i.e., already widespread), good dispersal capacity, and short generation time, at the expense of species with poor dispersal capacity and long generation time. For example, in the central North Island, increasing dominance will likely occur in species such as *Kunzea ericoides* (A.Rich.) J.Thompson (kanuka), *Leptospermum scoparium* J.R. et G.Forst. (manuka), and *Pseudopanax* spp., and to a lesser extent *W. racemosa* and the podocarps. We predict an initial decline in *Nothofagus* spp. and *Libocedrus bidwillii* Hook.f. (kaikawaka). The position of *B. tawa*, which is currently widespread, is equivocal given the substantial decline in numbers of its main dispersal agent, the New Zealand pigeon.

Rates of change will be governed not only by dispersal capacity, but also by the availability of new sites for seedling establishment, and will thus depend at many sites on mortality of the current occupants. Given the lack of evidence for increased mortality from physiological stress caused by temperature increases alone (Larcher 1983), delays until new sites become available are likely to approach the same order of magnitude as the typical longevity of the current site occupants. Some exceptions to this generalisation are noted below.

Examination of historical data indicates that migration rates for most species are unlikely to be sufficiently high to enable movement to all potential new sites in step with rises in temperature. For example, a 3°C rise in temperature by 2050 would require a potential latitudinal shift of 750 km at a rate of 12.5 km/year, or an altitudinal shift of 600 m at a rate of 10 m/year. In contrast, *Nothofagus* spp. have been shown to migrate at rates of only 0.05–0.1 m/year (Rogers 1989; Haase 1990). Migration rates for other species are not well known and are difficult to quantify. Some species may not establish until a suitable understorey vegetation has developed. Bird-dispersed species such as the podocarps, species with fine

wind-dispersed seeds such as *W. racemosa*, and *Metrosideros* spp. are undoubtedly capable of much faster migration than *Nothofagus* spp. Their rates of migration probably approach or perhaps even exceed those for European and North American species which, after the last glacial period, moved at rates of up to 2 km/year (Roberts 1989). However, rates of migration even in these species are likely to be too slow to keep up with the rate of warming except where migration has a substantial upslope component (Davis 1989). Where forest species invade currently non-vegetated sites, significant lag times may result from the need for soil development to progress sufficiently to support tree growth (Webb 1986).

Several factors, either singly or in combination, are likely to result in major forest disturbance, with a risk of the forest being replaced, at least for some period, by non-forest vegetation. Forest instability can be caused by the inability of new species to migrate at rates fast enough to occupy potential new sites as they become available. This may occur when:

- Small patches of forest become isolated from seed sources of likely replacement species, e.g., small remnants of forest vegetation in non-forested landscapes;
- Species are dependent on latitudinal (longer-distance) rather than altitudinal (shorter-range) migration, e.g., foothill forests of the main axial ranges;
- Forest patches occur with a narrow temperature range resulting from small area and/or little altitudinal variation, i.e., with little capacity for within-forest movement, and thus dependent on migration from other forest patches;
- Forests are dependent on replacement by species with low dispersal capacity, e.g., forest growing adjacent to *Nothofagus* forest, but on colder sites (upslope);
- Adjacent sites with suitable replacement species are absent, e.g., low-altitude coastal sites at northern ends of islands.

Replacement by exotic species is also a possibility. Factors predisposing existing forests to collapse over time periods shorter than the normal lifespan of the current forest dominants are:

- Widespread abiotic disturbance events, e.g., the cyclone-damage-prone *Nothofagus*-dominant forests of the central North Island axial ranges;
- Susceptibility of trees to physiological stress and hence to early mortality.

The latter is more likely to be a factor in forests dominated by species which are at the upper limit of their temperature range (lower latitude/altitude) and/or towards the lower limits of their rainfall range—the impacts of this would be exacerbated in floristically simple forests.

These factors point to some natural forest communities which may be particularly subject to negative impacts resulting from climate change. For example, over large areas of lowland New Zealand, and particularly in the North Island, there are only small scattered remnants of formerly extensive forests. A combination of geographical isolation from suitable seed sources, a dependence on latitudinal migration, and often narrow within-patch temperature range could lead to the current high conservation values of such remnants being severely threatened. At the other extreme, the relatively slowly dispersing *Nothofagus* spp. often form extensive, floristically simple forests, and occupy many sites with a high natural frequency of abiotic disturbance (e.g., Shaw 1983). If future disturbances or physiological stress result in mature tree collapse on sites where *Nothofagus* regeneration is climatically inhibited,

migration of possible replacements will be slowed, not because of forest fragmentation but by limitations on the speed at which suitable canopy replacements can migrate the necessary distances, perhaps through surviving intact *Nothofagus* forest. In extensive mountainous country where migration routes may be confined to warmer valley-bottoms, effective migration distances may be much greater than straight-line distances.

### Plantation Forests

Ninety percent of the plantation forest area grows with present-day mean annual temperatures between 10° and 15°C, and 35% between 10° and 11°C (Fig. 3). The latter consists of plantations in Clutha-Central Otago, Coastal-North Otago, Aorangi, Canterbury, Nelson, Wanganui, Hawke's Bay, Bay of Plenty, and Waikato. Plantations with mean annual temperatures less than 10°C are confined to Southland, Clutha-Central Otago, and Aorangi. The forest with the lowest mean annual temperature (8.0°C) is at Naseby in Clutha-Central Otago. Plantations with mean annual temperatures exceeding 15°C are all in the Bay of Plenty, Waikato, Auckland, and Northland regions, and the forest with the highest mean annual temperature (16°C) is at Aupouri in Northland. It is important to note that the mean annual temperature at the warmest site is 8°C warmer than that at the coldest site.

Mean minimum temperature in the coldest month of the year (the average of the lowest screen temperatures in the coldest month) is below 0°C for 92%, and between 0° and -2°C for 33% of the plantation area (Fig. 4). It is significant that mean minimum temperatures in

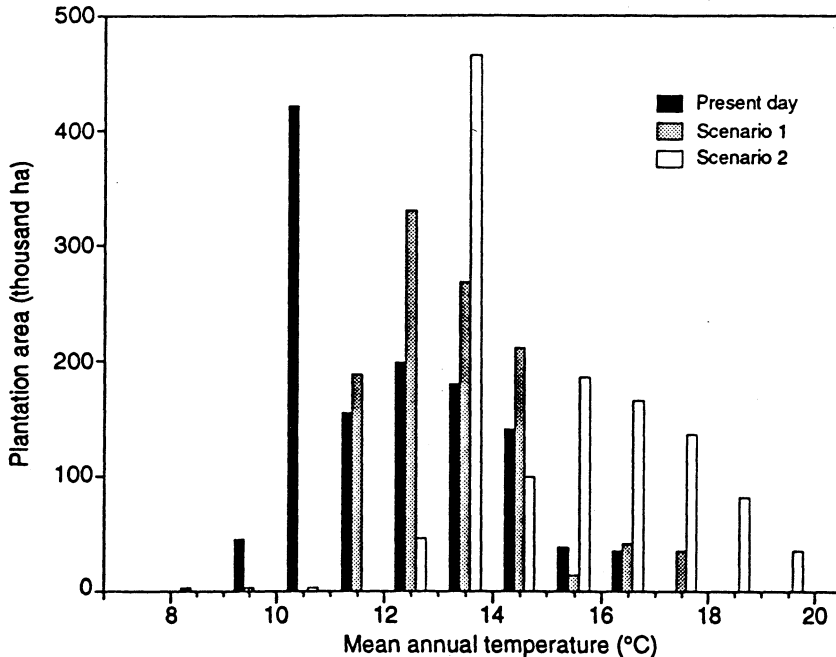


FIG. 3—Distribution of plantations of *Pinus radiata* in New Zealand in relation to present-day mean annual temperature, and with temperatures projected to occur during the period 2030 to 2050, using the “most likely scenario” (1) and “alternative warm scenario” (2).



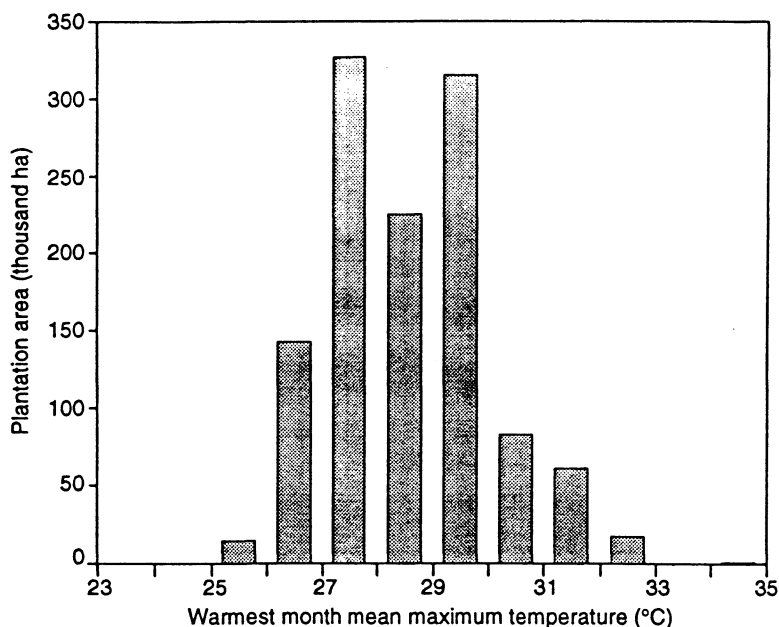


FIG. 4—Distribution of plantation areas of *Pinus radiata* in New Zealand in relation to the present-day mean maximum temperature in the warmest month.

the coldest month are between  $-5^{\circ}$  and  $-8^{\circ}\text{C}$  for 48% of the plantation area. The forest with the lowest mean minimum temperature in the coldest month ( $-9.6^{\circ}\text{C}$ ) is at Naseby in Clutha-Central Otago. Mean maximum temperature in the warmest month of the year (the average of the highest temperatures in the warmest month) does not exceed  $30^{\circ}\text{C}$  for 87% of the plantation area, and is between  $27^{\circ}$  and  $30^{\circ}\text{C}$  for 72% of the plantation area (Fig. 5). The forests with the highest mean maximum temperature in the warmest month ( $34.3^{\circ}\text{C}$ ) are in North Canterbury.

The distribution of forest area in relation to mean annual rainfall is shown in Fig. 6. Mean annual rainfall is between 1250 and 2250 mm for 75% of the plantation area. Mean annual rainfall exceeding 2250 mm is confined to a small (2%) area of forests at Hokitika and Greymouth in the West Coast region. Forests at the driest sites, where mean annual rainfall is less than 750 mm, are all in the Clutha-Central Otago, Coastal-North Otago, Aorangi, and Canterbury regions. The forest with the lowest mean annual rainfall (343 mm) is at Alexandra in Clutha-Central Otago.

Using the “most likely” and the “alternative warm” scenarios for changes to climate estimated on a regional basis, the distribution of plantation forest area in relation to temperature and rainfall for the middle of the next century are also shown in Fig. 3 and 6.

The most significant effect on the forest resource is the estimated increase in mean annual temperature. The lowest mean annual temperature for all forests, (except for 2551 ha at Naseby) is expected to increase to between  $11^{\circ}$  and  $12^{\circ}\text{C}$  for Scenario 1, and between  $12^{\circ}$  and  $13^{\circ}\text{C}$  for Scenario 2 (Fig. 3). For Scenario 1, more of the present-day plantation area is expected to experience mean annual temperatures between  $11^{\circ}$  and  $16^{\circ}\text{C}$ , but the mean

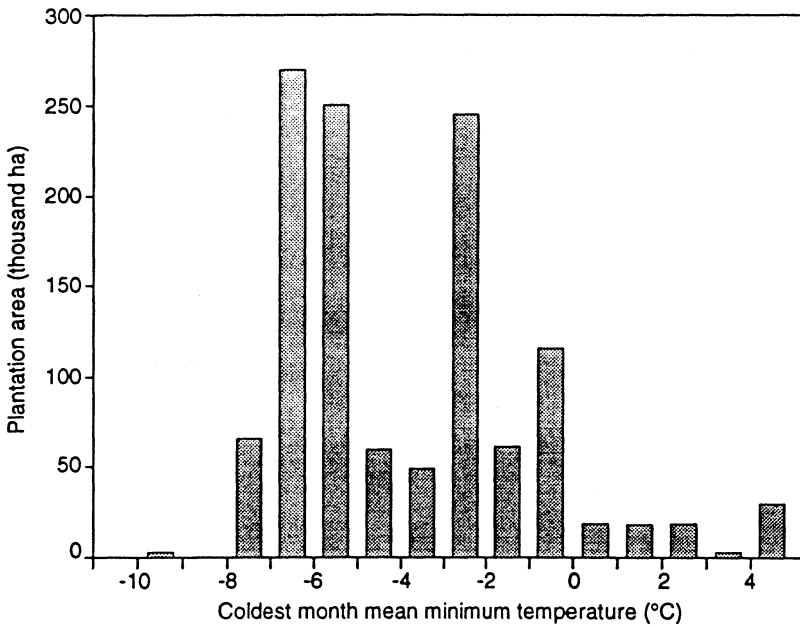


FIG. 5—Distribution of plantation areas of *Pinus radiata* in New Zealand in relation to the present-day mean minimum temperature in the coldest month.

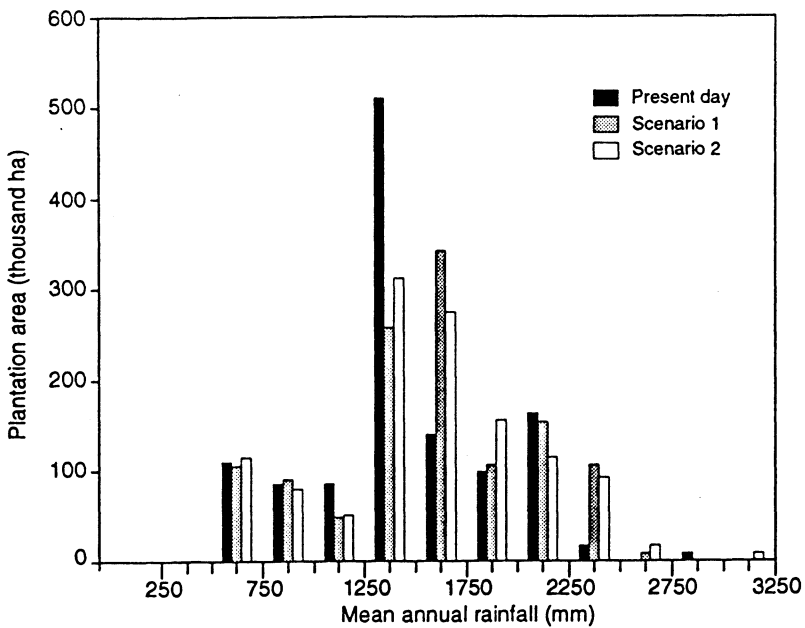


FIG. 6—Distribution of plantations of *Pinus radiata* in New Zealand in relation to present-day mean annual rainfall, and with the rainfall projected to occur during the period 2030 to 2050, using the “most likely scenario” (1) and “alternative warm scenario” (2).

annual temperature is expected to exceed current maximum values for only 3% of the plantation area at Aupouri Forest in Northland. However, if conditions estimated for Scenario 2 occur, then 96% of the plantation area will experience mean annual temperatures above 13°C and the area of forests experiencing mean annual temperatures above 17°C (which exceeds current maximum values in the present climate) will be 21%; of this, 10% is located in Northland with the remainder in the northern half of the North Island.

The effects of changes in rainfall on the forest resource are expected to be much less than the effects of temperature (Fig. 6). For both climate change scenarios there is a noticeable decrease in the plantation area which will experience a mean annual rainfall of between 1250 and 1500 mm, but more of the plantation area is likely to experience mean annual rainfall greater than 1500 mm (54% and 59% for Scenarios 1 and 2 respectively, compared with 35% in the present-day climate). Plantations in dry areas are not likely to benefit since increased rainfall is not predicted for these areas.

In contrast with natural forests, plantation species are selected intensively to achieve desirable rates of production, tree form, and wood quality characteristics. The time taken for each new generation of improved *Pinus radiata* is much less than the rotation time and requires about 10 to 12 years. Grace *et al.* (1991) argued that, because each generation of trees is grown in the climate which incorporates the most recent changes, the programme of "recurrent selection" which is already practised, will continue to provide genotypes which are already those best suited to the new climatic conditions. In this way, climate change is already built into the genetic improvement programme.

Whether the climatic limits for the growth of even the most suitable genotypes of *P. radiata* will be reached within the lifespan of current plantations at present day sites is a concern. The results from Fig. 6 suggest that rainfall amount and distribution are unlikely to change sufficiently to cause sites to be unsuitable for *P. radiata*. However, the projections of increase in temperature do provide concern. Both climate change scenarios show that all plantations will be experiencing higher temperatures (Fig. 3). Hunter & Gibson (1984) suggested that the optimum temperature for height growth in *P. radiata* is 12°C. The optimum temperature for *P. radiata* height growth in Australia was estimated to be 14°C (Booth & Saunders 1980). However, it is likely that the optimal temperatures for height growth and for productivity are different. Measurements in controlled environments showed that there was a significant increase in carbon balance for *P. radiata* foliage with day temperatures up to 25°C as long as night temperatures did not exceed 12°C (Rook & Corson 1978). If temperature increase occurs as suggested in Scenario 2, then the entire plantation area will be growing with daily mean annual temperatures exceeding these optima (Fig. 3).

Using data from sites elsewhere the world, it has been suggested that the climatic limits for economically acceptable growth rates for *P. radiata* in plantations are broad, i.e., mean annual temperature between 11° and 18°C, with a daily average maximum in the warmest season of 20° to 30°C, a daily mean minimum in the coldest season of -2° to 12°C, a mean annual rainfall between 650 and 1600 mm which is evenly distributed through the year with the dry period (< 40 mm/month) not exceeding 3 months (Booth 1990). Some of the warmest sites where plantations of *P. radiata* var. *binata* (Engelm.) Lemmon have been established are in Queensland, Australia (Huth 1982; actual temperature data not provided). *Pinus radiata* height growth was not seriously impaired at Woolgoolga arboretum in Queensland

where the mean annual temperature was 18.8°C and mean annual rainfall 1570 mm with a marked summer maximum (I.R. Hunter, unpubl. data). However, at an elevation of 1000 m on the Nadarivatu plateau in Fiji, where the mean annual temperature is 21°C, *P. radiata* height growth was restricted to 4 to 5 m at age 20 years (I.R. Hunter, pers. comm.). These results suggest that growth of *P. radiata* is adversely affected, but is still likely to be economically feasible, at sites where mean annual temperatures exceed about 19°C.

It is clear that the plantation areas most likely to be affected adversely by climate change are in Northland and Auckland where present-day mean annual temperatures are well above the reported optima for productivity, and approach the maximum limits for economically feasible production. Productivity in these areas is high, but less than that at other good North Island sites. Shula (1989) analysed data from the Forest Research Institute's Permanent Sample Plot system to identify sites where productivity of *P. radiata* was particularly high. For the 10 most productive sites in the country (defined by a mean annual increment in excess of 40 m<sup>3</sup>/ha/year) the mean annual temperature range is between 9.8° and 13.7°C and the mean annual rainfall between 1100 and 1200 mm (New Zealand Meteorological Service 1983). Only one of these forests, at Glenbervie, is in Northland. Clearly, there are many factors which could contribute to the observation that maximum productivity does not occur in forests in Northland, but this could be at least partly attributable to higher temperatures.

## CONCLUSIONS

The analyses used in this paper have enabled us to make initial predictions of the impacts of climate change on natural and plantation forests in New Zealand. However, these predictions are based on very limited data and the models have not been tested widely. The limitations of our approach need to be stated clearly. For example, the analysis of natural forest response assumes that species distributions are currently in equilibrium with current climate variables, i.e., they do not bear major imprints from past events such as climatic extremes or other major landscape-level disturbances. If this assumption is incorrect, predictions of change in species distributions will be unreliable, unless interpreted in the light of these historical events. In addition, predicted changes for natural forests take account of neither the tolerance of species to climates in which they do not currently occur, nor the effects of competition between species. This is because climatic surfaces describe the realised, rather than the fundamental niche of species, i.e., rather than indicating the potential climatic range of a species, they describe the climate over which a species is more competitive than other species (Austin & Smith 1989).

Predictions based on mean annual temperature and rainfall should be treated with caution, when the seasonality in these components and extreme values are not considered. No account of changes in such factors as disease and insect attack, nutrition, weed competition, and wind damage on forests is included. There is no consideration of the rate of acclimation of processes (relating to productivity, migration, for example) that will take place within species or genotypes in response to changing climate. As currently used, neither approach considers the responses of species to increased carbon dioxide concentration, including any interactive effects of carbon dioxide increases on plant responses to climatic variables.

Considerable further research is required to improve the certainty of these estimates. For more detailed predictions to be made for natural forest communities, information will be

required not only on current relationships between vegetation and climate, but also on the physiological response of plant species to changing climatic and carbon dioxide regimes, and the dynamic processes by which adjustment to new climatic regimes occurs (Ojima *et al.* 1991; Woodward & Diament 1991).

Management priorities for the remaining natural forests are currently oriented to conservation and watershed protection. Although the impacts of a changing climate will be more indirect than those on agriculture and plantation forestry, management intervention to protect and maintain current values may be necessary. However, such intervention must be preceded by development of clear objectives. For example, at a community level, there will need to be a clear recognition that the changes occurring in forest composition are an inevitable response to a changing environment. In contrast, intervention to overcome the effects of removal of former migration pathways (for example, by past agricultural development) may be considered to be a valid and necessary management action.

At a species level the choices will be more difficult. Decisions will have to be made concerning the need for intervention by moving populations of species which are at risk by virtue of factors such as current poor population status, or low dispersal capability. These decisions will have to balance the desire to conserve particular species against the likely impacts of artificial establishment on the composition of the surrounding communities. Given the relatively long life-span of most natural forest trees, there is probably little urgency for intervention, at least for several decades. The exception is where forest mortality is accelerated by extreme climatic events.

Analyses of the relationships between climate and productivity and wood quality of the plantation forest resource in relation to current climate variables have already been undertaken. For example, Jackson & Gifford (1974) took data on periodic volume increment for *P. radiata* at 132 sites from the maximum range of climates in New Zealand and showed that 66% of the variability (after age effects had been removed) could be accounted for by mean annual precipitation, seasonal rainfall distribution, seasonal departures of ambient temperatures from postulated optima, and the other site factors which were effective soil depth, and nitrogen and phosphorus availability. Hunter & Gibson (1984) sampled 290 plots of *P. radiata* across New Zealand and used principal components analysis to account for differences in site index (mean top height of trees in a stand at 20 years). Site index was predicted to increase with increasing rainfall and decrease with the departure from an optimum mean temperature. These approaches need to be extended to predict the effects of future climate scenarios on tree growth and wood quality and this will require the continued availability of comprehensive mensurational data sets.

There is an urgent need to determine the physiological response of plantation species and genotypes to increasing temperature and carbon dioxide concentration, and interactions. This will involve a major commitment of resources. Continuation of the long-term mensurational databases is essential at sites where the forest ecosystems are particularly at risk, to ensure that response to changing climate is recorded. This programme should include regular, extensive measurements of tree performance (e.g., diameter and height measurements) in combination with periods of intensive activity which are used to investigate processes and dynamics, in relation to climatic variables. Predictions of growth in a future climate will also be required at sites where forests have not yet been established.

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## REFERENCES

- AUSTIN, M.P.; SMITH, T.M. 1989: A new model for the continuum concept. *Vegetatio* 83: 35–47.
- BARLOW, E.W.; CONROY, J. 1988: Influence of elevated atmospheric carbon dioxide on the productivity of Australian forestry plantations. Pp. 520–33 in Pearman, G.I. (Ed.) "Greenhouse: Planning for Climate Change". CSIRO, East Melbourne.
- BOOTH, T.H. 1990: Mapping predictions for climatically suitable regimes for planting tree species at the global scale. *Forest Ecology and Management* 36(1): 47–60.
- BOOTH, T.H.; MCMURTRIE, R.E. 1988: Climate change and *Pinus radiata* plantations in Australia. Pp. 535–45 in Pearman, G.I. (Ed.) "Greenhouse: Planning for Climate Change". CSIRO, East Melbourne.
- BOOTH, T.H.; SAUNDERS, J.C. 1980: Land evaluation for forestry. Pp. 116–23 in "Plantation Forestry. What Future ?" Proceedings of the Combined Conference of the Institute of Foresters Australia and the New Zealand Institute of Foresters.
- BOX, E.O. 1981: "Macroclimate and Plant Forms: An Introduction on Predictive Modelling in Phytogeography". Junk, The Hague.
- EMMANUEL, W.R.; SHUGART, H.H.; STEVENSON, M.P. 1985: Climate change and the broad scale distribution of terrestrial ecosystem complexes. *Climatic Change* 7: 29–43.
- DAVIS, M.B. 1989: Lags in vegetation response to greenhouse warming. *Climatic Change* 15: 75–82.
- GRACE, J.C.; CARSON, M.J.; CARSON, S.D. 1991: Climate change—Implications for *Pinus radiata* improvement. *New Zealand Journal of Forestry Science* 21: 123–34.
- HAASE, P. 1990: Environmental and floristic gradients in Westland, New Zealand, and the discontinuous distribution of *Nothofagus*. *New Zealand Journal of Botany* 28: 25–40.
- HOLDRIDGE, L.R. 1967: "Life Zone Ecology". Tropical Science Centre, San Jose, Costa Rica.
- HOLLINGER, D.Y. 1988: Impact to forestry in New Zealand of increasing carbon dioxide and associated climate effects. Pp. 211–3 in "Climate Change. The New Zealand Response". Ministry for the Environment, Wellington.
- 1990: Forest Ecosystems. Pp. 69–77 in "Climate Change Impacts on New Zealand". Ministry for the Environment, Wellington.
- HUNTER, I.R.; GIBSON, A.R. 1984: Predicting *Pinus radiata* site index from environmental variables. *New Zealand Journal of Forestry Science* 14: 53–64.
- HUTCHINSON, M.F. 1988: A new objective method for spatial interpolation of meteorological variables from irregular networks applied to the estimation of monthly mean solar radiation, temperature, precipitation and windrun. In Fitzpatrick, E.A. (Ed.) "Proceedings of a United Nations University Workshop on Need for Climatic and Hydrologic Data in the Agriculture of South-East Asia". Canberra, 12–15 December 1983. United Nations University, Tokyo.
- HUTH, J.R. 1982: *Pinus radiata* var. *binata* trial plantings in south-east Queensland. *Department of Forestry, Queensland, Australia, Research Note No. 37*. 8 p.
- JACKSON, D.S.; GIFFORD, H.H. 1974: Environmental variables influencing the increment of radiata pine. I. Periodic volume increment. *New Zealand Journal of Forestry Science* 4: 3–26.
- JONES, P.D.; WIGLEY, T.M.; FOLLAND, C.K.; PARKER, D.E.; ANGELL, J.K.; LEBEDEFF, S.; HANSEN, J.E. 1988: Evidence for global warming in the past decade. *Nature* 332: 790.

- LARCHER, W. 1983: "Physiological Plant Ecology". Second edition. Springer-Verlag, Berlin.
- LEATHWICK, J.R.; MITCHELL, N.D. 1992: Forest pattern, climate, and vulcanism in central North Island, New Zealand. *Journal of Vegetation Science* 3: 603–16.
- McCULLAGH, P.; NELDER, J.A. 1983: "Generalized Linear Models". Chapman and Hall, London.
- McGLONE, M.S. 1988: New Zealand. In Huntley, B.; Webb, T. III "Vegetation History". Kluwer Academic Publishers.
- MINISTRY OF FORESTRY 1991: "New Zealand Forestry Statistics 1991." Ministry of Forestry, Wellington.
- MITCHELL, N. D. 1991: The derivation of climate surfaces for New Zealand, and their application to the bioclimatic analysis of the distribution of kauri (*Agathis australis*). *Journal of the Royal Society of New Zealand* 21: 13–24.
- NEILSON, R.P. 1987: Biotic regionalisation and climatic controls in western North America. *Vegetatio* 70: 135–47.
- NEW ZEALAND FOREST SERVICE 1986: "Forests of New Zealand". Forest Service Mapping Series 9.
- NEW ZEALAND METEOROLOGICAL SERVICE 1983: "Summaries of Climatological Observations to 1980". Government Printer, Wellington. 172 p.
- NORTON, D.A. 1985: A multivariate technique for estimating New Zealand temperature normals. *Weather and Climate* 5: 64–74.
- NOVIS, J.; TURLAND, J.; COLLINS, J. 1989: "A National Exotic Forest Description". Ministry of Forestry, Wellington. 108 p.
- OJIMA, D.S.; KITTEL, T.G.F.; ROSSWALL, T.; WALKER, B.H. 1991: Critical issues for understanding global change effects on terrestrial ecosystems. *Ecological Applications* 1: 303–15.
- PRENTICE, I.C. 1986: Vegetation response to past climatic variation. *Vegetatio* 67: 131–41.
- ROBERTS, L. 1989: How fast can trees migrate? *Science* 243: 735–7.
- ROGERS, G. 1989: Beech and conifer community interactions in Moawhango Ecological Region, North Island, New Zealand. *New Zealand Journal of Ecology* 12: 47–61.
- ROOK, D.A.; CORSON, M.J. 1978: Temperature and irradiance and the total daily photosynthetic production of the crown of a *Pinus radiata* tree. *Oecologia (Berlin)* 36: 371–82.
- ROYAL SOCIETY OF NEW ZEALAND 1988: "Climate Change in New Zealand". 28 p.
- SALINGER, M.J. 1988: New Zealand climate: Past and present. Pp. 17–24 in "Climate Change. The New Zealand Response". Ministry for the Environment, Wellington.
- SALINGER, M.J.; HICKS, D.M. 1989: Regional climate change scenarios. Working scenarios prepared for members of the Impacts Working Group, New Zealand Climate Change programme. 27 p.
- SALINGER, M.J.; PITTOCK, A.B. 1991: Climate scenarios for 2010 and 2050 AD in Australia and New Zealand. *Climatic Change* 18: 259–69.
- SHAW, W.B. 1983. Tropical cyclones: Determinants of pattern and structure in New Zealand's indigenous forests. *Pacific Science* 37: 405–14.
- SHULA, R.G. 1989: The upper limits of radiata pine stem-volume production in NZ. *New Zealand Journal of Forestry* 34: 19–22.
- SOWELL, J.B. 1985: A predictive model relating North American plant formations and climate. *Vegetatio* 60: 103–11.
- TURLAND, J.; NEUMANN, A. 1991: "A National Exotic Forest Description as at 1 April 1990". Edition 7. Ministry of Forestry, Wellington.
- WALTER, H. 1979: "Vegetation of the Earth and Ecological Systems of the Geo-Biosphere". Second edition. Springer-Verlag, New York.
- WEBB, T. III. 1986: Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* 67: 75–91.
- WOODWARD, F.I. 1986: "Climate and Plant Distribution". Cambridge University Press.
- WOODWARD, F.I.; DIAMANT, A.D. 1991. Functional approaches to predicting ecological effects of global change. *Functional Ecology* 5: 202–12.