SIMULATING NEW ZEALAND FOREST DYNAMICS WITH A GENERALIZED TEMPERATE FOREST GAP MODEL

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Abstract. A generalized computer model of forest growth and nutrient dynamics (LINKAGES) was adapted for the temperate evergreen forests of New Zealand. Systematic differences in species characteristics between eastern North American species and their New Zealand counterparts prevented the initial version of the model from running acceptably with New Zealand species. Several equations were identified as responsible, and those modeling available light were extended to give more robust formulations.

The resulting model (LINKNZ) was evaluated by comparing site simulations against independent field measurements of stand sequences and across temperature and moisture gradients. It successfully simulated gap dynamics and forest succession for a range of temperate forest ecosystems in New Zealand, while retaining its utility for the forests of eastern North America. These simulations provided insight into New Zealand conifer-hardwood and beech species forest succession.

The adequacy of the ecological processes, such as soil moisture balance, decomposition rates, and nutrient cycling, embodied in a forest simulation model was tested by applying it to New Zealand forest ecosystems. This gave support to the model's underlying hypothesis, derived from LINKAGES, that interactions among demographic, microbial, and geological processes can explain much of the observed variation in ecosystem carbon and nitrogen storage and cycling. The addition of a disturbance option to the model supported the hypothesis that large-scale disturbance significantly affects New Zealand forest dynamics.

Key words: biomass accumulation; forest dynamics; forest gap model; individual-based model; LINKAGES; LINKNZ; model evaluation; New Zealand; nitrogen cycle; simulation; temperate evergreen forest.

INTRODUCTION

Individual-based forest simulation models predict the dynamics and structure of complex forest ecosystems. Worldwide, long-term forest composition and forest species distributions are under pressure from continuing large-scale anthropogenic effects. Because forest simulation models are ecosystem based, they can provide both predictions of forest response to these impacts and a consistent synthesis of the ecological processes involved (Rastetter 1996). Such properties make them a vital part of any assessment of ecosystem response to global change (Reynolds et al. 1996, Shugart and Smith 1996).

The structure of most simulation models of forest succession can be traced back to those developed to reproduce the population dynamics of trees in mixed-species forests of northeastern North America (Botkin et al. 1972, Shugart and West 1977). This approach tracked the development of each individual plant throughout its life cycle, with forest dynamics simulated by calculating the competitive interrelationships among trees in a restricted area, similar to that resulting from the gap in a forest canopy formed by the death or removal of a large canopy tree. By simulating a sufficient number of gaps, the dynamics of the forest are reproduced (Yamamoto 1992). This concept is supported by various plant succession studies, which show that changes in a forest ecosystem may be described by averaging the growth dynamics in gaps of different successional ages (Watt 1947, Bray 1956, Curtis 1959, Forman and Godron 1981).

Forest gap simulation models have been developed to predict long-term impacts on forest ecosystems caused by blight, harvest management, past climates, animal browse, pollution, and large-scale disturbance by fire or storm, and to predict transients in species composition and forest structure due to changing climate, (e.g., Shugart and West 1977, Aber et al. 1979, Solomon et al. 1981, Pastor and Post 1988, Bugmann 1996). Shugart and Smith (1996) compiled a list of 37 such models developed to simulate vegetation dynamics in environments ranging from cool Northern Hemisphere boreal forest to warm subtropical Australian rain forest. Almost half of these models are dedicated to North American vegetation (80% of these in eastern forests), with the other models predicting forest composition and dynamics in central and northern Europe, Australasia, Africa, and Asia.
Comparisons have shown that a forest gap model developed for one geographical area is unlikely to contain all of the ecological processes required to successfully simulate forest composition and structure for another area (Bugmann et al. 1996). This is partly because, despite a common lineage, models formulate the basic processes of species establishment, growth, and mortality variously. Models also vary by the way in which resource limitations alter growth, by the species’ life history attributes employed, and by the depth of physiology incorporated. Not all models explicitly maintain a soil moisture balance or a litter decomposition–soil nutrient cycle.

In an effort to better determine the potential role of climate change and other exogenous factors on New Zealand forest development, we extended an eastern North American simulation model (Pastor and Post 1985) for New Zealand’s forests. In doing so, we evaluated the ecological generality of functions and algorithms developed originally for the eastern North American forests, and gained insight into several long-running debates about ecological processes in New Zealand forests.

The nature of New Zealand’s topography, climate, and forest characteristics indicated which ecosystem processes to model. New Zealand’s small group of islands (landmass 270,000 km²) have variations in climate, geology, and soil that offer a wider range of habitats than many much larger landmasses (Wardle 1984, Molloy 1988). The three main islands (North, South, and Stewart) span 1500 km (13°) of latitude and have a maritime climate, with sea level temperatures ranging from warm temperate in the north (mean annual temperature (MAT) ~ 15°C) to cold temperate in the south (MAT ~ 10°C). New Zealand is tectonically active, with mountain building continuing at rates of up to 12 mm/yr (Whitehouse 1988). About 60% of the land is >300 m above sea level, and 70% is defined as hilly or steep (Molloy 1988). The varied topography cuts across the prevailing westerly winds, modifying land temperatures and causing strong rainfall gradients. The North Island has a central volcanic plateau with an average elevation of 500 m and main axial mountain ranges running northeast to south. Rainfall exceeds 1600 mm/yr in these areas and can reach 6000 mm/yr. There are also sizable areas of lowlands and coastal plains. The South Island has a young mountain range running 700 km north to south. The many summits >3000 m create strongly differentiated climatic gradients. In the eastern lee of the South Island range, rainfall drops to a low of 300 mm/yr, whereas on the windward side in Westland and Fiordland, it may reach 12,000 mm/yr near the ranges.

The forests of New Zealand are dominated by long-lived evergreen species (Wardle 1984, Wardle 1991). *Nothofagus* (beech) species characterize many forest types, occurring either in pure associations (46% of the remaining forested area) or in mixed forest (22% of remaining forest area). Beech species predominate in mountain regions of both main islands. Their wide ecological ranges enable their frequent occurrence in montane zones as well as lowland areas. In the northern warmer areas (north of 38°S), the conifer *Agathis australis* dominates the forests in association with a mixture of hardwoods, podocarp, and beech species. Further south, lowland forests are characterized by emergent, long-lived, evergreen podocarp species *Dacrydium, Podocarpus, and Prumnopitys*. These are associated with a diverse group of broad-leaved hardwoods (*Beilschmiedia, Metrosideros, and Weinmannia*), characteristic of the main canopy (Ogden et al. 1996).

The strong rainfall gradients and dry summer climates influence species composition and led us to consider models with a site water balance (e.g., Pastor and Post 1986, Botkin and Nisbet 1992). The young landscapes and generally infertile forest soils in New Zealand (Molloy 1988, Wardle 1991) similarly required models that relate soil nutrient status to species composition and forest stature (e.g., Aber et al. 1982, Pastor and Post 1986, Bonan 1990). We chose the LINKAGES gap model (Pastor and Post 1986, Post and Pastor 1996) because it included these ecosystem processes without excessive data requirements. It has explicit feedbacks between light, water, and nitrogen availability, and their effects on stand composition and productivity. Previous gap models have related soil nutrient status to tree growth by species-specific sigmoid equations that reach maximum values at the highest reported basal area, or biomass, for a given region. The LINKAGES model eliminates these site-specific maxima by explicitly simulating water and nutrient availability and using them to influence tree growth (Post and Pastor 1996). However, the model lacks some recent modifications in allometric relationships, growth equations, and spatially explicit modeling of the light environment (e.g., Leemans and Prentice 1987, Martin 1992, Pacala et al. 1993, Prentice et al. 1993, Bugmann 1996). A complete description of LINKAGES is given in Pastor and Post (1985).

Our model, LINKNZ, is a version of LINKAGES generalized for New Zealand forest conditions, with species parameters obtained from an alternative database of New Zealand species (G. M. J. Hall and D. Y. Hollinger, unpublished manuscript). Here, we examine how well LINKNZ simulates forest patterns and reproduces forest characteristics in a range of broad-leaved hardwood and conifer forest types throughout New Zealand. The model presented is intended as a basis for future development. Some characteristics of New Zealand tree species differ profoundly from those of eastern North American species. Therefore, we were careful to extend, rather than modify, the mechanisms of competition or nutrient cycling. This preserved the model’s original ability to reproduce dynamics of the forests of eastern North America and allowed a com-
parison of results with LINKAGES. Our intention was to produce a more generally applicable forest gap model.

METHODS

Model description

The LINKAGES model (Pastor and Post 1985, 1986) shares a common structure with the JABOWA/FORET class of stochastic tree population models that predict ecosystem dynamics through interactions between the forest and available resources (Botkin et al. 1972, Shugart and West 1977). The model simulates, on a yearly cycle, the establishment, growth, and mortality of all individual trees in a 1/12 ha plot (0.083 ha), adjusted by the effects of climate, soil properties, and competition. Plot size corresponds to the average gap created by a dominant tree in eastern North American forests (Shugart and West 1977). Initial diameter at breast height (dbh) is stochastically set between 1.27 cm and 1.42 cm. Monthly rainfall and temperature variables, together with soil moisture capacity and wilting point, determine available site moisture. As the canopy forms and develops, light availability to each tree changes, affecting growth rates and the establishment of new trees. Available soil nitrogen is initialized for the site and then determined annually by external inputs, losses due to leaching, and dynamics associated with processes of immobilization and mineralization during litter decomposition (Post and Pastor 1996). Available soil nitrogen then affects tree growth and stand composition, which, in turn, alters litter quantity and quality and modifies decomposition rates (Pastor and Post 1985).

A sufficient number of growing seasons, or annual cycles, was set to allow modeled forest biomass at each site to settle into an approximate steady state. The longevity of several widespread, dominant New Zealand tree species (G. M. J. Hall and D. Y. Hollinger, unpublished manuscript) led us to run the model for 2000 annual cycles, rather than the 250–400 considered sufficient for eastern North American species by Pastor and Post (1985), or the 1000-yr period used by Pacala et al. (1993). We retained this 2000-yr time frame when simulating stochastic whole-stand disturbances, to allow long-lived individuals in any undisturbed stands to complete at least one life cycle.

The stochastic nature of the model requires that more than one plot be simulated to obtain an adequate description of forest composition and structure (Yamamoto 1992). We generated 50 plot successions on each site to smooth anomalous events.

Because of its LINKAGES heritage, LINKNZ also tracks details of soil organic matter and nitrogen pools, as well as site water balance. Typically, both soil organic matter and soil N accumulate on a plot for several centuries until reaching an approximate steady state. By contrast, the estimates of transpiration depend only on the physical environment. These outputs assist in the understanding of factors regulating vegetation at different sites, but insufficient New Zealand data prevented further evaluation.

Site data

Latitude, monthly temperature, monthly rainfall, and growing season data were obtained from New Zealand Meteorological Service climate reports (1969–1986). Soil moisture holding capacity and wilting point were set according to broad soil type and soil moisture deficit maps (Molloy 1988), and knowledge of the seven test sites. The initial organic matter (74.5 Mg/ha) and N levels (1.64 Mg/ha) were left as the model default values.

Species data

We selected 72 tree species considered fundamental to the structure and functioning of New Zealand native forest ecosystems, using a reference file of all woody species found on surveys (Hall 1992). These species included early successional species, understory species, and many major canopy species occurring throughout New Zealand forests. We also included four common and widespread tree fern species, *Cyathea smithii*, *C. dealbata*, *C. medullaris*, and *Dicksonia squarrosa*, because of their influence on patterns of succession in New Zealand forests (Wardle 1991). They are treated by the model in the same way as tree species. Optimal growth constants were calculated from the equations of Botkin et al. (1972) from species maximum dimension and longevity. Species used are listed in the Appendix.

Model parameters generated from the species’ life history attributes included maximum height, maximum diameter, maximum longevity, limits of annual growing degree-day sums, shade and nutrient tolerances, establishment conditions and rates, and various canopy, foliage, and litter properties. Data and methods of obtaining parameters are described in G. M. J. Hall and D. Y. Hollinger (unpublished manuscript).

EXTENSIONS TO LINKAGES

The LINKAGES model, as presented by Pastor and Post (1986), required modifications to its slow-growth, available-light, and decay-rate conditions to reproduce forests characteristic of New Zealand sites. Many major forest species did not feature in the simulations. For example, at Riverhead near Auckland, LINKAGES limited species composition to the large conifer *Agathis australis* and two hardwoods, *Beilschmiedia tawa* and *B. tarairi*, and excluded the common podocarp species *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *P. taxifolia*. Further south at Taupo, LINKAGES predicted that the hardwood *B. tawa* would dominate and exclude all the common podocarp species. This pattern was repeated at other sites throughout the country, with site occupation being captured by one or two hardwood
or beech species and other widespread species failing to establish.

Slow-growth conditions

The LINKAGES model tests the growth of a tree independently of age and employs conditions common to many other models. If the resource-limited diameter increment is less than a fixed minimum of 1 mm/yr (Botkin et al. 1972, Shugart 1984, Botkin and Nisbet 1992), or <10% of the maximum increment for its size (Solomon 1986), the model defines this as a poor growth year for the stem. If a tree grows poorly for two consecutive years, the probability of survival is reduced so that it has a <1% chance of surviving 10 consecutive years of poor growth.

This “poor-growth” condition is too restrictive for modeling several slow-growing New Zealand species. The clearest case is that of the long-lived conifer Halocarpus biformis, with a highest recorded growth increment of 0.8 mm/yr (Wardle 1991), preventing LINKAGES from establishing it at all. Under LINKAGES, the widespread, dominant conifers of the Poaceae remain in a quiescent state (<1.35 m tall), making only limited growth for decades until an opportunity is provided by the death of canopy trees (Wardle 1984). Nothofagus fusca, normally one of the faster growing dominant species (Stewart and Rose 1990), may grow in diameter by only 0.8 mm/yr under a dense canopy, with 70% of the poles in a typical stand passing through this stage (Kirkland 1961). Baxter and Norton (1989) show a similar growth release behavior for Dacrydium cupressinum and Quintinia acutifolia, in which ring widths of young trees are <0.5 mm/yr under an intact canopy, but increase to widths of 2–4 mm/yr after the overstory trees are removed.

To minimize alterations to the model, we retained the same slow-growth conditions of LINKAGES when maximum diameter increments exceeded 2.5 mm/yr, or when maximum longevity was attained. For maximum increments <2.5 mm/yr, growth was defined as slow only when resource-limited increments were <10% of the maximum increment. The 2.5 mm/yr threshold was chosen by comparison against optimal growth increments recorded for a range of New Zealand tree species (G. M. J. Hall and D. Y. Hollinger, unpublished manuscript). Species with a maximum diameter increment exceeding 2.5 mm/yr will have, at some point, the same tests for slow growth as in LINKAGES, whereas those that never attain this increment have the 1 mm/yr fixed minimum waived. These conditions allowed the slowest growing species, including several in the Poaceae, to establish and move through the slow-growth phase without excessive mortality.

Available light at the forest floor

The light passing through a canopy can be modeled, using the Beer-Lambert law, as

\[ I = I_o \exp(-k \cdot \text{LAI}) \]  

where \( I \) is the light intensity below the canopy; \( I_o \) is the light intensity above the canopy; \( k \) is an extinction coefficient that is a function of foliage angle distribution, spatial dispersion, and optical properties; and LAI is the leaf area index in square meters of foliage per square meter of ground (Monsi and Saeki 1953). The LINKAGES model calculates \( I \) as a percentage of full sunlight. This value is used to determine whether there is sufficient light for new individuals to become established on the plot, and as a growth multiplier for seedlings of those species that can establish. In LINKAGES, it is calculated (Aber et al. 1982) as:

\[ I = \exp(-F/93750) \]  

where \( F \) is the foliage mass in grams per plot, and the divisor 93750 is a factor that accounts for the size of the plot (833.3 m²) and converts the mass of the foliage into an effective leaf area index. The per meter conversion factor of 112.5 (93750/833.3) is thus the product of the leaf mass per unit area (SLM) and the reciprocal of the extinction coefficient, \( k \). Whittaker et al. (1974) used a value of \( <92 \text{ g/m}² \) for northern hardwoods foliage, implying that the implicit value of \( k \) from Aber et al. (1982) is \( <0.8 \).

New Zealand forests are predominantly evergreen, with high specific leaf mass, in contrast to the predominantly deciduous eastern North American forests. Consequently, LINKAGES underestimates available light in New Zealand sites for a given foliage mass, with the result that canopy species prevent any new establishment. We rewrote Eq. 2 as

\[ I = \exp(-F/[833.3(1/0.8)\cdot\text{SLM}]) \]  

to take account of the variation in SLM, which was an implied constant in LINKAGES, and then used our measured SLM values.

Canopy openings and the decay rate

Within LINKAGES, canopy openings are assumed to increase decay rates because of microclimatic changes. The model relates closed-canopy leaf production, \( L_o \), to available water for plant growth, \( W_s \) (Pastor and Post 1984), as

\[ L_o = 1.54 + 0.457W_s \]  

It then compares this year’s leaf litter (\( L_o \)) with \( L_o \) to construct a decay multiplier that increases decomposition under canopies with low leaf area (Aber et al. 1982). For soils of high water-holding capacity, the multiplier ranges from 1.0 (\( L_o = L_o \)) to 2.0 (no canopy); for low water-holding capacity, it ranges from 1.0 to 1.25 (Pastor and Post 1986).
duction is too low for most New Zealand forests; $L_c$ exceeds $L_a$, causing the model to set the decay multiplier to 1.0 and so nullify any gap effect. Field examples show that Daniel (1975) estimated $L_a$ as 3.2 Mg·ha$^{-1}$·yr$^{-1}$ in a New Zealand podocarp–broad-leaved forest; Benecke and Evans (1987) established that $L_a$ = 6.4 Mg·ha$^{-1}$·yr$^{-1}$ from a Nothofagus truncata forest; and Hollinger et al. (1994) obtained $L_a$ = 5.9 Mg·ha$^{-1}$·yr$^{-1}$ from a mature N. fusca stand. Leaf production may be greater in New Zealand forests because of a longer growing season, combined with the evergreen habit of most tree species.

Over a 2000-yr run of the model, simulations at a warm-temperate species-rich forest site at Riverhead, Auckland showed that the original decay multiplier was nullified in 99.9% of years on soils of low water-holding capacity, and in 66.2% of years on soils of high water-holding capacity. To compensate for differing New Zealand forest leaf production values and to retain Eq. 4 for American species, a scaling factor was applied to $L_a$. This was obtained by multiplying each plant’s litter mass by the average northern hardwood foliage mass of 92 g/m$^2$ (Whittaker et al. 1974) and dividing by the species’ SLM. Over the simulated period, the model calculated mean values for $L_c$ of 2.70 Mg·ha$^{-1}$·yr$^{-1}$ on low-water-holding capacity soils and 2.77 Mg·ha$^{-1}$·yr$^{-1}$ on high-capacity soils. The SLM adjustment rescaled these mean values downward by nearly 50%, making them comparable with the $L_c$ of old-growth American forests in Eq. 4, and activating the decay rate multiplier in New Zealand forest sites. After this adjustment, the decay-rate multiplier on the simulated Riverhead forest plot was negated on just 0.3% of the annual cycles.

**Disturbance**

Pollen, charcoal, and fossilized plant fragments point to a long history of change in New Zealand indigenous forests. Forest disturbances have been due to physical factors associated with steep mountain slopes, and include volcanism, periodic fire, forest dieback, windthrow, drought, flooding, and snow damage (Wardle 1984). We added a basic mechanism to LINKNZ to simulate disturbanc. The type (wind or fire) and the mean disturbance return time can be set in the site parameters. The LINKNZ model will trigger that type of disturbance with a probability annually that is the reciprocal of the disturbance frequency. After windthrow, all trees on the plot are assumed to be dead and all biomass, including belowground root mass, is returned to the site for decomposition–nutrient cycling. After fire, all trees are assumed to be dead and the larger biomass components are returned to the site. The biomass and N in foliage and twigs are presumed to be volatilized and lost from the site.

Revisions made to the LINKAGES code (Pastor and Post 1985) gave a threefold improvement in execution speed. The LINKNZ program, species data, and site data will be made available, subject to a “fair use” policy, on the web site (http://www.landcare.cri.nz).

**MODEL EVALUATION**

Evaluation of forest ecosystem gap models is not straightforward. To construct definitive tests of simulated forest dynamics, several stands would have to be monitored for long periods while they were returning to old-growth forest. Even in well-observed eastern North American forests, a lack of historical data on succession has been acknowledged (Pacala et al. 1993). In addition, Rastetter (1996) has noted that each alternative used to evaluate modeled ecosystem response to global change fails to provide a severe and crucial test. Partly, this is due to difficulties in locating past or present ecosystem states comparable to those expected under climate change. For instance, how can valid data be obtained for evaluating long-term vegetation responses to increased CO$_2$ when short-term chamber experiments are still inconclusive? We adopt recent evaluation methods for forest gap models to evaluate the ability of the model under current climates, but acknowledge that theoretical difficulties remain.

Shugart (1984) and Shugart and Smith (1996) discuss procedures used for testing the results of gap models. Most include assessing the model’s abilities to reproduce “target patterns” of stand or tree biomass increments, stand structure (basal area, density, stem diameter distributions) or composition (relative basal area, relative density) for stands of known age, successional trends in a chronosequence of stands, and forest response to disturbance as a “natural” experiment. Bugmann (1996) tested model predictions of species composition, biomass, and distribution on a range of sites in the European Alps. We assess LINKNZ similarly by comparing output with general characteristics of forest vegetation at sites throughout New Zealand. These sites are located across both temperature and precipitation gradients in habitats varying from diverse-species warm-temperate forests to limited-floristic cool-temperate forests (Table 1). Pacala et al. (1993) tested their spatially explicit model against data from a short chronosequence (up to 100 yr), and against a long-term succession, by comparing species composition and basal area. We compare our model through time against studies of forest successional development on landslides in southwestern New Zealand (Mark et al. 1964, 1989; Stewart 1986).

Comparisons of models and methods can give confidence if underlying methods are independent (Rastetter 1996). We compare simulated long-term dynamics against successional sequences deduced by methods based on empirical data and models unrelated to LINKNZ (e.g., Ogden 1983, Wardle 1984, Ogden et al. 1987, Burns and Smale 1990). Bugmann et al. (1996) compare versions of forest gap models showing changes due to additional features. We briefly compare results between our model and a test of an allometry-
based gap model on a New Zealand site (DeVelice 1988).

Finally, we present and discuss model results for forests where large-scale disturbance appears to play a role in shaping forest structure.

RESULTS

General patterns of forest succession and composition

The model reproduces the broad patterns of forest succession and composition at a variety of test sites. At Riverhead, Auckland, a silty clay loam soil texture (field moisture capacity 38.3 cm, wilting point of 20 cm) was chosen to represent moister, valley soil conditions. From the simulations, mean relative stem densities at 25-yr intervals for the main species (with mean biomass > 0.01 Mg·ha⁻¹·yr⁻¹) were clustered using a group-average linkage with a gamma similarity coefficient (SYSTAT 1997). This gave three groups of species at the 0.8 similarity level. The early-arriving group (1A) separated at the 0.45 similarity level into primarily short-lived, small trees (group 1A) and longer lived tall trees (group 1B). Initially, modeled primary succession proceeds through the fast-growing group 1A species, especially *Leptospernum scoparium* and *Kunzea ericoides*, with *Aristotelia serrata* also present for the first 25 yr (Fig. 1). Included in group 1A is the slow-growing *Phyllocladus trichomanoides*, which can maintain a longer presence. The relative density of these pioneer species drops rapidly after 25–50 yr, returning only when large canopy gaps occur after year 500.

The massive conifer *Agathis australis* attains dominance in >90% of the simulated plots by year 300 and, like the group 1A pioneers, begins at a high density. Over the first ~200 yr, *Agathis* also replaces group 1B, early-establishing hardwood species including *Weinmannia silvicola*, *Knightia excelsa*, *Elaeocarpus dentatus*, and the beech *Nothofagus truncata* (Fig. 1). The model suggests, however, that *Agathis* does not regenerate well in situ, with its relative density declining steadily for >500 yr and its biomass dropping until it disappears after 1700–1800 yr. As *Agathis* declines after 500–700 yr, the forest becomes co-dominated by species from groups 1B and 2, forming an *Agathis*/hardwood community with an increasing podocarp component (Figs. 1 and 2A). The group 2 species, *Beilschmiedia tawa* and *B. tarairi*, rise in numbers, reaching 30% of total biomass between years 500 and 800, and then decline to hold a near-constant 10% of total biomass after 1200 yr, as the longer lived group 3 podocarps emerge. Of these, *Dacrydium cupressinum* gains slowly in relative density and biomass after group 1A species disappear, while *Prumnopitys ferruginea* and *P. taxifolia* increase rapidly as *Agathis* wanes. In the absence of a large disturbance, such as fire, these podocarp species (with a small hardwood component) are predicted to eventually characterize the forest.

Our simulations indicate that, at this warm New Zealand site, maximum forest biomass is reached between 250 and 450 yr, while *Agathis* dominates. During that period, the model predicts a mean basal area of 62 m²/ha (Fig. 2B), of which *Agathis* contributes 58 m²/ha. This compares well with a mean basal area of 57 m²/ha for *Agathis*, observed in 25 mature (mean age 327 yr) stands (Ahmed and Ogden 1987).

With a drier soil (moisture capacity 22.9 cm, wilting point 10.4 cm), depicting ridge conditions at Riverhead, *Agathis* is predicted to persist at the expense of the group 2 hardwoods. The simulation (not graphed) produces a 6.5% higher mean *Agathis* biomass, with a lower maximum and a smoother decline. The hardwood species *Beilschmiedia tawa* and *B. tarairi*, which favor more fertile soils and are less tolerant of water stress than *Agathis*, drop in mean biomass by >50%, from 9.8% to 4.3%. In comparison, the three major podocarp species retain 31–33% of total biomass. The drought-tolerant *Prumnopitys taxifolia* prospers at the expense of both *D. cupressinum* and *P. ferruginea*.

In the cooler climate further to the south, near Taupo
Fig. 1. Relative stem densities of key species on modeled plots using climate and soil data from Riverhead, Auckland. Other species of lesser importance on the modeled plots include: *Elaeocarpus hookerianus* in group 1B, *Quintinia serrata* in group 2, and *Podocarpus totara* and *Podocarpus hallii* in group 3. In this and all subsequent simulations, the values shown are the means from 50 simulated 1/12 ha plots. Minimum and maximum mean percentages of total stems are given for each species.

(Fig. 3A), modeled primary succession on silty clay loam soil proceeds again through *Kunzea ericoides* with *Leptospermum scoparium*, and *Aristotelia serrata*. *Weinmannia silvicola* is replaced by the cooler climate species *W. racemosa*, and warmer temperate species such as the hardwood *Beilschmiedia tawa* and the dominant conifer *Agathis* fail to establish. The common North Island hardwood *B. tawa* retains a small, constant biomass (~6%) throughout the simulation period. In the first 100 yr, modeled plots are dominated by *Weinmannia racemosa*, *K. ericoides*, and *Elaeocarpus* species. These species make up >70% of total biomass at year 100, reduce to 50% by year 200 as the podocars *Dacrydium cupressinum*, *Prumnopitys taxifolia*, and *P. taxifolia* increase, and become a minor component at 1% by year 500. Modeled community composition is similar to that at lakeside sites in the Taupo area (Wardle 1984, Clarkson and Nicholls 1992). The successional patterns resemble a sequence described by Wardle (1991) for parts of this central North Island volcanic plateau area with a deep tephra soil, characterized by *D. cupressinum*-dominated mixed-podocarp forest establishing by 200–300 yr and developing by 400–500 yr into a large, mature podocarp–broad-leaved forest.

By contrast, simulations carried out using the cooler climate conditions for Reefton (typical of the South Island west coast of New Zealand) suggest that the emergent podocarp *Dacrydium cupressinum*, in association with the common hardwood *Weinmannia racemosa*, will more quickly dominate plots in this area (after the initial establishment of *Aristotelia serrata*, *Leptospermum scoparium*, and *Kunzea ericoides*). The model shows *Prumnopitys* and *Podocarpus* species, followed by *Nothofagus* species, beginning to establish after ~200 yr (Fig. 3B). Minor canopy and subcanopy species include *Libocedrus bidwillii*, *Quintinia acutifolia*, *Metrosideros umbellata*, *Pseudopanax crassifolius*, and *Cyathea* species. Simulations for the Reefton area show *Nothofagus menziesii* as the prime beech...
species. Apart from *N. fusca* (to be discussed), forest composition agrees with descriptions of the area (Wardle 1984). The drop-off in biomass over 30 yr at about year 900 represents mortality of the last of the original cohort of the long-lived, dominant *D. cupressinum*. The gap model predicts that the eventual “steady-state” forest composition of the major species at Taupo and Reefton may be similar (Fig. 3A, B), with comparable patterns for *W. racemosa* and the podocarp species *D. cupressinum, P. ferruginea*, and *P. taxifolia* at both sites. Slight differences are evident, with Reefton predicted to have a larger beech component and *B. tawa* restricted to Taupo, as observed in nature.

The model generates a similar forest 200 km south at Franz Josef (Fig. 3C), where the mean annual temperature is only slightly lower than in Reefton (Table 1). Early succession at this site is started by *Leptospermum scoparium* and *Aristotelia serrata*, rather than *Kunzea*, as at the more northern sites. A similar amount of *Nothofagus menziesii* is predicted in forest at Franz Josef, as for Reefton (Fig. 3B, C). However, Franz Josef is located within the 150-km stretch of the South Island west coast where *Nothofagus* is absent (referred to as the “beech gap”). Excluding beech species from the model at Franz Josef does not alter the forest dynamics greatly, and correctly predicts a *Dacrydium cupressinum*-dominated podocarp forest (Fig. 3D). Other species include *Weinmannia racemosa, Quintinia acutifolia, Pseudowintera colorata*, and *Cyathea smithii*.

Still omitting beech species from the model, we simulated climate conditions several hundred meters upslope of the Franz Josef meteorological station by reducing mean monthly temperatures by 2°C. At this upslope site, a mixed hardwood–podocarp forest is simulated with *Metrosideros umbellata, Weinmannia racemosa, Podocarpus hallii*, and *Phyllocladus aspleniifolius var. alpinus* (Fig. 3E). Other species present include *Griselinia littoralis, Libocedrus bidwillii*, and *Pseudowintera colorata*. This change in species composition with elevation corresponds with that commonly observed along the western slopes of the Southern Alps in New Zealand (e.g., Wardle 1991). The total biomass in these simulated slope forests is about two-thirds that estimated for the lowland podocarp forests. This reduction is caused partly by a change in species composition from the large, lowland podocarp, *Dacrydium cupressinum*, to the smaller-statured podocarp, *P. hallii*, with the broad-leaved hardwood *W. racemosa*, and is exacerbated by the decline in biomass of the dominant *M. umbellata*. *Metrosideros* initially dominates the forest, reaching ~200 Mg/ha after 250 yr, but is gradually replaced by *Podocarpus hallii* after 500 yr.

On the drier east side of the Southern Alps, the model simulates very different forests from those on the wetter west side (Fig. 3F, G). At the driest site (mean precipitation 635 mm/yr) near Twizel, on a sandy soil, the model generates a forest dominated by *Podocarpus hallii*, with a small amount of *Nothofagus solandri* var. *cliffortioides*, *Phyllocladus aspleniifolius var. alpinus*, and *Prumnopitys taxifolia*. Early succession at this site is dominated by *Leptospermum scoparium* and *N. solandri* var. *cliffortioides*. The simulated biomass of these plots is ~220 Mg/ha. Although there is no forest at present around Twizel, on adjacent slopes there is abundant charcoal evidence for a *P. hallii* forest before the arrival of Polynesian settlers in New Zealand (Molloy et al. 1963, Wells 1972). On drier, cooler sites, pollen and charcoal evidence from the foot of the Ben Ohau Range near Twizel record a *P. alpinus*-dominated scrub with a lesser *P. hallii* component and traces of *N. solandri* var. *cliffortioides* (McGlone and Moar 1998).

At the higher elevation Craigieburn site (Fig. 3G), on a sandy-loam soil, the model generates a mixed *Nothofagus solandri* var. *cliffortioides–N. menziesii* forest where there is presently solely *N. solandri* var. *cliffortioides*. This modeled forest exhibits interesting dynamic behavior, and will be discussed in more detail (see Natural monocultures).

**Forest succession on landslides in Fiordland**

Simulated forest succession at Lake Thompson (using climate data from the West Arm, Manapouri station) allowed comparison with several detailed studies of succession in the area (Mark et al. 1964, 1989, Stewart 1986). Qualitatively, much of the early pattern of succession observed by Mark et al. (1964, 1989) was reproduced by LINKNZ, with *Aristotelia serrata* and *Leptospermum scoparium* being replaced by *Weinmannia racemosa, Nothofagus solandri* var. *cliffortioides, Metrosideros umbellata*, *Griselinia littoralis*, and even-
FIG. 3. Modeled aboveground biomass for sites around New Zealand (see Appendix for species); the contribution of each species to the total biomass is cumulative. (A) Taupo: the initial peak ("Others") includes Aristotelia serrata, Leptospermum scoparium, and Kunzea ericoide, followed later by a small amount of Beilschmiedia tawa and assorted minor species. (B) Reefton: the initial peak ("Others") includes A. serrata, L. scoparium, and K. ericoide. (C) Franz Josef, with the full species list: other species include L. scoparium, A. serrata, Quintinia acutifolia, Pseudowintera colorata, and Cyathea smithii. (D) Franz Josef without beech: as for Fig. 5C, but without Nothofagus in the seed pool. (E) Franz Josef without beech and with climate conditions at −2°C: early successional species (bottom peak) are L. scoparium and A. serrata; other species include Griselinia littoralis, P. colorata, and Phyllocladus alpinus. (F) Twizel: other species include P. alpinus, Prumnopitys taxifolia, and L. scoparium. (G) Craigieburn: the mountain climate produces a mixed N. solandri var. cliffortioides—N. menziesii forest, with a small amount of L. scoparium and P. alpinus (bottom line).
Our simulation reproduced the initial relative density of 20% for 50±80 yr old stands, but predicted only 5% for this species after 50 yr. Despite these differences, the simulation of an adjacent mature Nothofagus menziesii–Weinmannia racemosa–Pseudowintera colorata forest is still very acceptable (e.g., Stewart 1986, Mark et al. 1989). With reference to species’ relative densities, we note that our modeled results are the average of 50 stands; individual stands can follow quite distinct trajectories from the mean.

**Effects of disturbance**

Introducing relatively infrequent stochastic disturbance (1/12 ha total plot blow-down on the average of 200–500 yr) results in simulated forests with a greater representation of early successional species and lower biomass than in forests where only individual tree gap replacement dynamics are allowed. This regime has the effect of not only increasing the number of gaps over time, but also dramatically altering the stand structure. Over time, a plot generally carries several trees so that, when one dies, any remaining individuals are free to respond, but under the blow-down scenario, all remaining trees on the plot are killed (e.g., Fig. 5A vs. Fig. 2A, and Fig. 5B vs. Fig. 3B). In these simulations, the long-lived podocarp species decline in absolute as well as relative importance, while other species tend to maintain absolute biomass and increase in relative representation.

This is illustrated at the Reefton site, which has a history of mass disturbances including two major earthquakes in the area during this century (Wardle 1984). When we imposed a mean disturbance return time of 300 yr and allowed fallen material to remain on site, predicted total biomass of Nothofagus species at Reefton increased from 5.5% without disturbance to 27.5%. The beech *N. fusca* is common in the area (Wardle 1984), but in simulations without disturbance, it was virtually absent (Fig. 3B). The introduction of disturbance allowed *N. fusca* to capture >12% of total biomass, increased *N. menziesii* from 5% to 16% of total biomass, and led to the establishment of a small amount of *N. solandri*. With this disturbance regime, the early-establishing and common hardwood *Weinmannia racemosa* retained a constant presence and more than doubled its share of biomass from 5.6% to 13.4%. These gains came at the expense of the podocarps, with the biomass of *Prumnopitys* species reduced by one-half and *Dacrydium cupressinum* reduced by one-third.
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**GENERALIZED FOREST GAP MODEL**

**FIG. 5.** Simulations of biomass in relation to stand age under stochastic whole-plot disturbance. The bottom line includes early successional and minor species. (A) Fire in Auckland, with a mean annual return time of 300 yr. (B) Windthrow in Reefton, with a mean annual return time of 300 yr.

...to 26%, compared to a scenario without random disturbance.

**DISCUSSION**

The lists of species and successional patterns generated by the model for different sites in New Zealand agree closely with those observed at the local sites (e.g., Wardle 1984, Wardle 1991). At the sites tested, the model does not establish any species where it does not belong, with the exception of the “beech gap,” to be discussed. For example, the commonly described pattern of colonization, which has the fast-colonizing *Kunzea ericoides* and *Leptospermum scoparium* acting as “nurse” species for *Agathis australis* or podocarps (Ogden 1983), is reproduced in the Riverhead, Auckland simulation (Fig. 2A), as is the eventual replacement of *Agathis* by hardwoods and podocarps (Ogden et al. 1987). In the initial 100–200 yr, the Riverhead simulation also shows the common hardwoods *Weinmannia silvicola*, *Knightia excelsa*, *Elaeocarpus dentatus*, the beech *Nothofagus truncata*, and *Phyllocladus trichomanoides* establishing in numbers, and then gradually being overtopped and replaced by *Agathis* (Fig. 1). This successional sequence in these warmer temperate forests is described by Ecroyd (1982) and Burns and Smale (1990). The model also reproduces observed changes in species composition for different soils. Drier soil sites favor longer term *Agathis* occupation, whereas moister soils suit hardwood species (Ecroyd 1982).

The biomass and basal area estimates produced by the model are more difficult to evaluate, but agree in general with published estimates. From a harvesting trial in a typical 130-yr-old *Agathis* stand in the Hunua Ranges south of Auckland, Madgwick et al. (1982) estimated the *Agathis* biomass component at ~132 Mg/ha. On *Agathis*-occupied plots, with Hunua climate data, the model predicts a mean ~133 Mg/ha *Agathis* component at 150 yr. Huge biomass is possible in clumped stands of mature *Agathis* forest (Wardle 1991). Hinds and Reid (1957) estimate that a representative area of a typical mature *Agathis* forest with 100 merchantable stems/ha could produce 400 Mg/ha, on average, of commercial timber. Madgwick et al. (1982) found that stemwood made up 64% of total *Agathis* biomass in their study; this factor generates an approximate total biomass estimate of 625 Mg/ha. This compares with the model estimate in which total *Agathis* biomass reaches a peak of 630 Mg/ha in 300–450 yr old stands. Near Riverhead, Ogden (1983) recorded basal areas of *Agathis* of 72 m²/ha for a ~300-yr-old stand and 55 m²/ha for a young ~120-yr-old “ricker” stand. In comparison, our model simulations predict lower mean basal areas of 62 m²/ha on 300-yr-old *Agathis*-dominated stands and 49 m²/ha at 125 yr (Fig. 2B). Burns and Smale (1990), on an intermediate-stage 200-yr-old site on the Coromandel Peninsula, obtained a total basal area of 62 m²/ha, of which 42% was contributed by *Agathis*. Our model, with their Coromandel site climate data, predicted a similar total stand basal area, but with an 89% *Agathis* component.

For Reefton, we estimated undisturbed mature podocarp–beech forest aboveground biomass at ~325 Mg/ha (Fig. 3B) and belowground biomass at ~300 Mg/ha. For periodically disturbed mature podocarp–beech forest, above- and belowground biomass was ~235 and ~260 Mg/ha, respectively. Beets (1980) recorded aboveground (living) and belowground (excluding logs) biomass values of 306 Mg/ha and 340 Mg/ha, which included 147 Mg/ha of roots, at a mature mixed-podocarp–beech site near Reefton. In the Craigieburn Range, several studies have investigated *Nothofagus solandri* var. *cliffortioides* aboveground biomass, finding values that range between 177 and 323 Mg/ha (Beenecke and Nordmeyer 1982, Schoenenberger 1984, Harcombe et al. 1998). Our simulated values range from 129 to 284 Mg/ha.

Although the model successfully simulates broad successional patterns within New Zealand forests, detailed patterns may not be exactly reproduced, particularly during the early-establishment stages. Forest gap models incorporate stochastic elements to mimic many ecosystem processes and produce multiple simulations to obtain average results and calculate confidence limits. Uncertainty in model data and possible errors in...
field data also obscure reconstructions of past events (Rastetter 1996). Deviations between model and reality result from a number of sources. These include potential errors in site parameters such as climate or soil water-holding capacity, errors in species parameters, and flaws in our understanding (and in modeling this understanding) of how site and species characteristics interact and affect forest growth.

The results from Lake Thompson are instructive. Our climate estimates for Lake Thompson are taken from a site 50 km distant, in an area of high relief and climatic extremes; our estimate of initial site fertility may also be imprecise. We use the same set of growth parameters for each species throughout New Zealand (ignoring ecotypic variation) and some of these parameters are relatively imprecise estimates. A chronic problem with testing gap models in this way is that the species potentially available on a plot exceed those that naturally occur (the model provides for an omnipresent seed source, ignoring seed dispersal mechanisms and differing arrival times). This results in a relatively high percentage of “other” species that may exist for only several years before dying off. In addition, during early establishment, the model initiates all individuals as equal-aged saplings with a mean stem dbh of 1.5 cm. Time required to reach this point is not explicitly accounted for and there can already be considerable age differences between individuals, depending upon their species’ growth characteristics.

Despite these problems, the detailed pattern of succession simulated for landslides near Lake Thompson is reasonable. The species characteristics given to LINKNZ were not altered nor were the species limited to those present in the Lake Thompson area. DeVelice (1988) presented a basic FORET-type model with allometric parameters set for the five tree species of greatest importance at the Lake Thompson landslides. Even so, his model overestimated the initial density of *Nothofagus solandri* var. *cliffortioides* and the subsequent density of *N. menziesii*. In these DeVelice (1988) simulations, *N. menziesii* accounted for nearly 50% of total stand density by year 80, whereas Mark et al. (1964, 1989) found that its density was generally <10% of the total. The LINKNZ model produced a better approximation to field counts of these *Nothofagus* species, and predicted the increases in *Pseudowintera colorata* over time that were noted by Mark et al. (1989). It did deviate from field observations by initially establishing podocarp species (not included by DeVelice 1988); although these species did not become a significant part of the site biomass until year 200 (Fig. 4B), they lowered relative density predictions for the hardwood species. The simulated early and numerous establishment of these bird-dispersed podocarp species lends support to the contention of Mark et al. (1989) that the initial floristics model of primary succession (Egler 1954), in which species arrive simultaneously and successively gain dominance according to their life history attributes, may not fully account for the early dynamics on these slip faces. In summary, although our results and those of DeVelice (1988) deviate in some details from the short-term pattern of succession reported by Mark and co-workers, the mature forest simulation of LINKNZ corresponded closely to that described by Stewart (1986) and Mark et al. (1989).

Having established the validity of the model for reproducing general successional patterns across a range of sites in New Zealand, we then used the model to provide some insights on several ongoing debates concerning ecological patterns and processes in New Zealand.

### Regeneration gap

There has been debate concerning the “lack” of regeneration in *Agathis australis* forests (for discussion, see Ecroyd 1982 and Ogden 1985). Our results, based solely on gap-phase replacement dynamics inherent in the model, support the primary succession theory of Egler (1954) and the early belief (Cockayne 1928) that *Agathis* is successional to a climax podocarp forest (Figs. 1, 2A) and that strongly *Agathis*-dominated forests would occur only in the first 400 yr after large-scale disturbance. The gap size and frequencies produced by the model are a consequence of the comparative life history attributes set for the trees that occupy the site. Thus, long-lived trees will produce gaps only infrequently; in the case of *Agathis*, this frequency is so low that there is sufficient time for the shade-tolerant hardwoods and podocarps to become well established, reducing the likelihood that enough light would penetrate through the understory of a tree-sized gap to permit abundant *Agathis* regeneration. In a study of *Agathis* treefall gaps, Ogden et al. (1987) found that *Agathis* established in only a few, enough to maintain a presence but not dominance. They estimated that, owing to its longevity (mean > 600 yr), *Agathis* could survive on any site up to 1500–2000 yr. The corresponding simulation (Fig. 2A), without large-scale disturbance, shows *Agathis* declining from an initial dominance, but remaining a significant component of the forest for nearly 1600 yr.

Many workers have pointed out the importance of larger scale, infrequent disturbance to New Zealand forest dynamics (e.g., Veblen and Stewart 1982, Ogden 1985), and have urged acceptance of “kinetic” models (e.g., Veblen et al. 1980) in which stochastic disturbance is accepted as a selective force. Ahmed and Ogden (1987) inferred from their study of *Agathis* population structure that episodic regeneration occurred at intervals of 100–300 yr. Our introduction of stochastic disturbance of this frequency into the dynamics of the model (Fig. 5A) resulted in stands where *Agathis* remains an important component of the forest. Without disturbance, *Agathis* biomass makes up ~44% of the total biomass at year 600 after most of the initial cohort
have gone, declining to zero by year 1800 (Fig. 2A). In the stochastically disturbed scenario (Fig. 5A), *Agathis* biomass remains at $\sim 33\%$ of total biomass over the entire interval between 600 and 1800 yr. Our results are consistent with the conclusion of Ahmed and Ogden (1987): *Agathis* is a successional species that maintains a strong presence in the forests of Northland because of repeated disturbance.

**“Beech gap”**

*Nothofagus* species are completely absent from a 150-km stretch along the central west coast of the South Island, and are also absent from Stewart Island, 40 km south of the South Island. Cockayne (1926) suggested that this absence could be the result of insufficient time for beech to have recolonized the area since the end of the last glaciation ($\sim 10,000$ yr BP). Our results for sites within the “beech gap,” such as Franz Josef and Hokitika (data not shown), lend support to Cockayne’s hypothesis. When beech is part of the available species pool, it can establish and become a permanent, if low-biomass, component of the forest. Even when beech availability on the site was delayed 1000 yr to allow the forest to fully establish first, LINKNZ indicated that a small amount of beech could establish. This suggests that poor modes of dispersal in beech may play a more significant role than any total inability to compete. Wardle (1964) also suggests that New Zealand beech may compete less effectively with existing vegetation where the rainfall is high, such as on the west coast, than in the drier conditions to the east of the axial ranges. The LINKNZ model supports this contention, because the simulations show that beech requires a longer period of time to become established in the “beech gap” sites than on the drier, cooler east side of the South Island in the Craigieburn Range (compare Fig. 3B, C with Fig. 3F, G).

Beech establishment in this region may also be influenced by the effects of stand-level disturbance on soil fertility. The model suggests that stochastic disturbances that create gaps larger than normal treefall size promote the establishment of some beech species. Wardle (1984) points out that beech can be outcompeted in low-elevation, high-rainfall areas owing to difficulties in finding suitable sites and increasing competition in the high-density, species-rich understories. Ogden (1988) notes that *N. fusca* prefers lower-fertility sites and would be expected to have difficulty establishing. At this low-elevation, low-fertility site, the model predicts that other species, such as the common hardwood *Weinmannia racemosa*, would capture the area and lead to the establishment of large, dominant podocarps such as *Dacrydium cupressinum*.

**Natural monocultures**

Our results for the Craigieburn forest show that biomass contributions of the beech species *Nothofagus solandri* var. *cliffortioides* and *N. menziesii* tend to oscillate out of phase with one another in a damped cycle of $\sim 500$ yr (Fig. 6A). An ecological interpretation of this behavior is that, as the fast-growing, light-demanding, even-aged stands of *N. solandri* var. *cliffortioides* thin, they become replaced by relatively even-aged stands of the shade-tolerant *N. menziesii*. When these *N. menziesii* stands senesce, the faster growing *N. solandri* var. *cliffortioides* begin to recapture the site. Because *N. menziesii* is longer lived and can continue to regenerate under its own canopy, these oscillations
lengthen and decrease in amplitude over subsequent generations.

This “counter-cyclical succession” is a consequence of the life history attributes of the two species most suited to the cool Craigieburn climate. Both species have wide, overlapping soil fertility, soil moisture, and climatic tolerances (Wardle 1984, Benecke and Allen 1992; G. M. J. Hall and D. Y. Hollinger, unpublished manuscript). In New Zealand, these species form almost continuous alpine and subalpine forests throughout the axial mountain ranges of both main islands. Wardle (1984) found that in mixed stands, dense, small-diameter (young) Nothofagus menziesii usually occur in conjunction with large-diameter (old) N. solandri var. cliffortioides and, conversely, stands with low numbers of large N. menziesii trees often have high densities of young N. solandri var. cliffortioides trees. Ogden (1988) further suggested that N. solandri var. cliffortioides will gradually be replaced by N. menziesii unless the stand is severely disturbed. In fact, the Craigieburn forests are essentially monocultures of N. solandri var. cliffortioides, with few other canopy species. Disturbance events such as wind, earthquake-triggered landslips, and heavy snowfall (Wardle 1984) frequently disrupt these subalpine and alpine forests on the eastern slopes of the South Island axial range. Age-diameter distributions indicate that stands may be severely damaged by gales at periods of ~120–150 yr, and stands suffer minor damage at intervals of 20–30 yr (Wardle 1984, Jane 1986, Harcombe et al. 1998). When we investigated the influence of disturbance on the dynamics and biomass of N. solandri var. cliffortioides–N. menziesii forests by adding stochastic disturbance (blowdown of whole-plot biomass) to the dynamics of the model, the counter-cyclical pattern of succession was removed (Fig. 6B). Furthermore, as the mean interval between disturbances decreased, the relative percentage and absolute amount of N. menziesii in the resulting stands decreased from a 70% dominance to <20% for mean intervals greater than one event every 120 yr (Fig. 7). This model behavior provides support for Wardle’s (1984) conclusion that stability favors N. menziesii and disturbance favors N. solandri var. cliffortioides, and suggests why N. solandri var. cliffortioides can be so dominant in disturbance-prone subalpine forests.

Conclusions

We evaluated the degree to which principles and relationships derived from North American studies could be used to simulate the structure and dynamics of New Zealand forest ecosystems. The characteristics of New Zealand tree species are significantly different from those of eastern North American trees. New Zealand species are generally long-lived evergreens with low N and high specific mass foliage that is retained in the canopy for several years. Yet, a model that was based on ecological processes of tree competition and growth, litter decomposition, and N cycling that originated primarily in North America and was designed to simulate the ecology of eastern North American species, only required minor modifications to acceptably simulate general forest patterns and processes across climatic gradients in a range of New Zealand forest types. The most significant modifications improved the way in which the predecessor model, LINKAGES, calculated the forest floor light environment and modified the slow growth rate conditions that trigger mortality.

Overall, our results tested the adequacy of the ecological processes embodied in forest simulators such as LINKAGES. They provided support for the model’s underlying hypothesis: interactions among demographic processes determining plant population structure, microbial processes determining N availability, and geological processes determining water availability explain much of the observed variation in ecosystem C and N storage and cycling (Pastor and Post 1985). In this framework, geology and climate act as constraints within which feedbacks between vegetation and light availability, and between vegetation and N availability, operate. By incorporating a simple disturbance regime into the model, we also supported the hypothesis that large-scale disturbance is of importance in shaping the dynamics and current composition of New Zealand forests (Veblen and Stewart 1982, Ogden 1985, Wardle 1991).

The LINKNZ model is a versatile simulation model of vegetation patterns and processes in New Zealand forests. It may find additional practical applications in investigating the impacts of climatic change, forest harvesting practices, forest restoration, or introduced animal impacts on the dynamics of indigenous vegetation. Furthermore, the modifications that we have incorporated should also improve the performance of the model in its original domain, the northeastern United States.

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APPENDIX

A list of the 76 New Zealand forest species selected for input to the LINKNZ forest gap model is available in ESA's Electronic Data Archive: Ecological Archives A010-001.