SORTIE/NZ model development

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Contents

Acknowledgement

1   Introduction

This document describes the structure of the model SORTIE/NZ (Figure 1) and its parameterisation in detail. SORTIE/NZ was implemented using the SORTIE-ND (www.sortie-nd.org) software, a descendant of the earlier SORTIE model (Pacala et al. 1996), but with a new architecture developed by C. Canham, L. Murphy, and M. Papaik (see http://www.sortie-nd.org/index.html). It consists of two main components: a graphical user interface (written in Java), and the core program (written in C++), which contains libraries of all of the different behaviours (submodels) that can be invoked during execution of a run.

The general structure of the model (see Figure 1) is based on the following behaviours:

Substrate behaviours.—The substrate behaviours simulate the dynamics of the forest floor on which seeds germinate and seedlings develop. The relative proportions of each kind of substrate are tracked in the Substrate grid.

Recruitment behaviours.—The number and spatial distribution of tree seedlings are predicted for each species from relationships with the adult-tree locations, size and abundance, and by the favourability of seedbed substrates (e.g. logs or mineral soil) for seedlings under varying light conditions.

Growth behaviours.—Species-specific equations predict the growth of seedlings or saplings based upon their size and light availability. The growth of trees is estimated based upon their diameter size and neighbourhood basal area as a measure of local crowding. Allometric relationships are used to convert tree diameter to tree height.

Mortality behaviours.—Seedling mortality is based upon the relationship between probability of mortality in relation to height and light availability for each species. Small seedlings with low light have a much higher probability of death. Sapling mortality is based on a mean mortality rate estimated from remeasurement of National Vegetation Survey Databank (NVS) plots in Southland (Wiser et al. 2001). Adult tree mortality was determined as a function of tree size also using NVS Databank plots from Southland.

Light behaviours.—Light availability patterns in the forest understorey are predicted as a function of size, canopy allometry, and spacing of trees in mapped stands, using species-specific light transmissions (Canham et al. 1999).

Disturbance behaviours.—This behaviour simulates the effects of earthquake disturbance. The parameterisation is based on data reporting the effects of an earthquake (Magnitude 6.7) on a pure mountain beech forest in 1994 (see Allen et al. 1999).

Harvesting behaviours.—SORTIE can implement complex silvicultural treatments. Harvest events are defined by species, time-step, level of harvest, type of harvest, and area harvested. Harvesting scenarios are based on the sustainable forest management prescription in the 1993 amendment to the New Zealand Forests Act 1949.

All these behaviours (or submodels), in turn, determine the distribution of trees at the beginning of the next time-step (here one time-step = 1 year). Relationships for these

behaviours are based upon detailed field measurements recently undertaken on infertile marine terraces in Waitutu Forest, Southland, New Zealand.
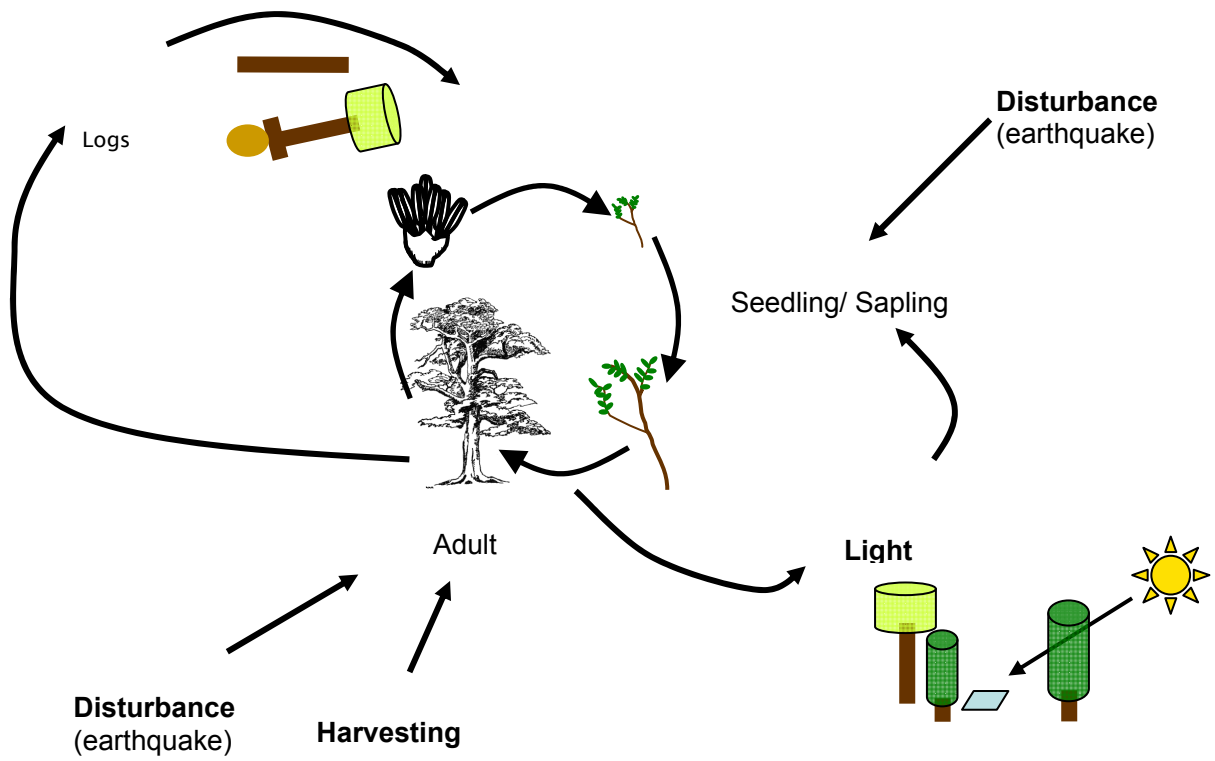
Figure 1 Schematic diagram of SORTIE/NZ.

2   Species list

The model focused on the seven dominant tree species (three podocarps, two beeches and two other angiosperms; see Table 1, Figures 2 and 3), which represent more than 98% of the total basal area at our study site (infertile marine terraces in Waitutu Forest, Southland, New Zealand; Coomes et al. 2005).

Table 1 Dominant tree species at Waitutu Forest, Southland, and associated acronyms

Species	Common name	Acronym
Dacrydium cupressinum	Rimu	DACCUP
Nothofagus solandri	Mountain beech	NOTCLI
Nothofagus menziesii	Silver beech	NOTMEN
Podocarpus hallii	Hall's tōtara	PODHAL
Prumnopitys ferruginea	Miro	PRUFER
Weinmannia racemosa	Kāmahi	WEIRAC
Metrosideros umbellata	Southern rātā	METUMB
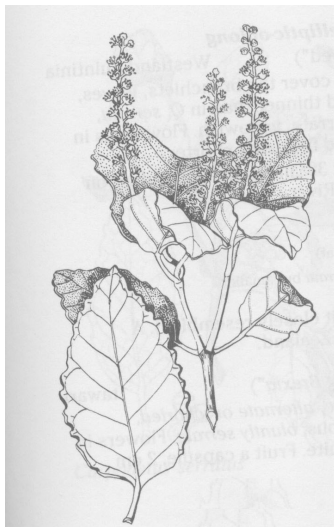
Weinmannia racemosa
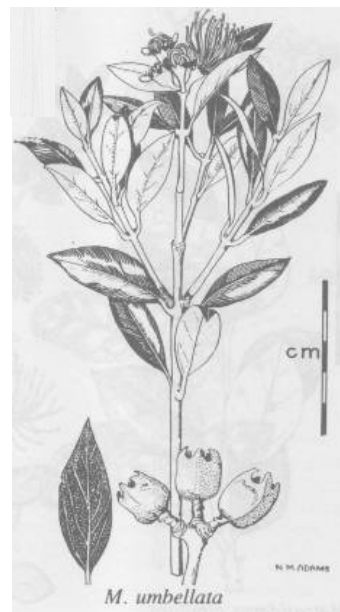
**Metrosideros umbellata
(Myrtaceae)**
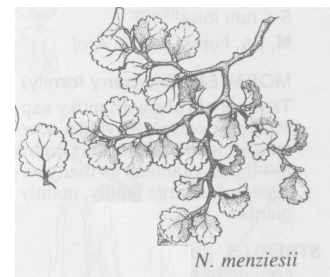
**Nothofagus menziesii
(Nothofagaceae)**
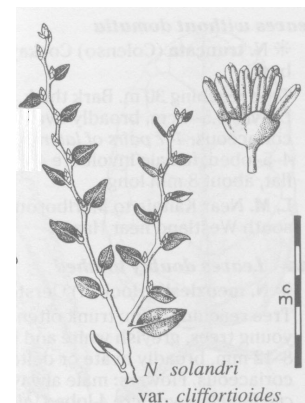
**Nothofagus solandri
(Nothofagaceae)**

Figure 2 Dominant angiosperm tree species at Waitutu Forest, Southland (from Poole & Adams 1963).
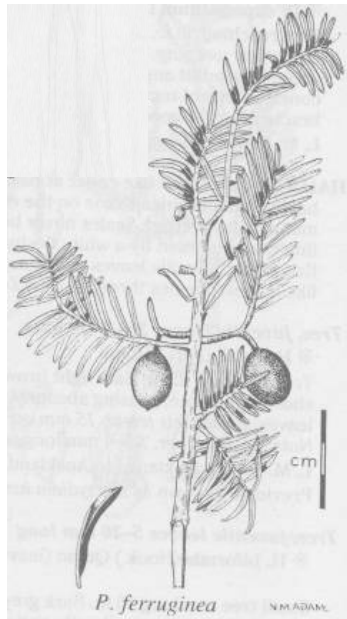
Prumnopitys ferruginea   **Dacrydium cupressinum**   **Podocarpus halli (Podocarpaceae)**
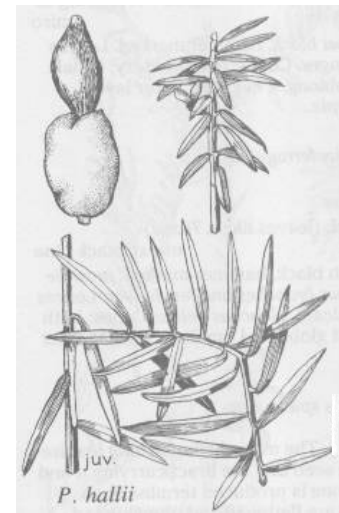
Figure 3 Dominant podocarp species at Waitutu Forest, Southland (from Poole & Adams 1963).

3   Tree life-history stages and allometry

3.1   Description of tree life-history stages

In SORTIE/NZ three life-history stages are used to describe the dynamics of a tree species: (1) seedling, (2) sapling and (3) adult tree. These life-history stages are defined as follows:

Seedling.—Seedlings are defined as being less than 1.35 m in height. The initial height of seedlings at time of establishment was set to 10 cm, to correspond with the minimum size of the seedlings used in the dataset for calibrating seedling growth and survival behaviours (we did that by setting the diameter at 10 cm height (D_{10}) of new seedlings to D_{10} initial ~ 0, as D_{10} initial = 0.01 cm).

Sapling.—Saplings are defined as having a diameter at breast height (DBH, at 1.35 m height) greater than 0 and less than the minimum adult tree DBH (10 cm). Seedlings and saplings are sometimes referred to collectively as 'juveniles'.

Adult.—Adults are defined as having a DBH ≥ 10 cm.

3.2   Allometry

Allometric functions are used in SORTIE/NZ to describe the relationships between various aspects of a plant's size and shape.. We present below the functions, and their parameterisation, for each life-history stage.

Seedling.—The relationship between height and diameter at 10 cm height (D_{10}) is represented by a linear function (Figure 4):

Height (H) = $a + b * D_{10}$

where: H is seedling height (in metres), a is the Seedling Linear Function Intercept, b is the Seedling Linear Function Slope, and D_{10} is diameter for seedlings. The intercept was fixed at 10 cm (i.e. a = 0.1 m), because the diameter was measured at a height of 10 cm in the field. The parameters (see Table 2) were estimated with the function lm in R, based on data from a seedling demographic study (Kunstler et al. 2009).
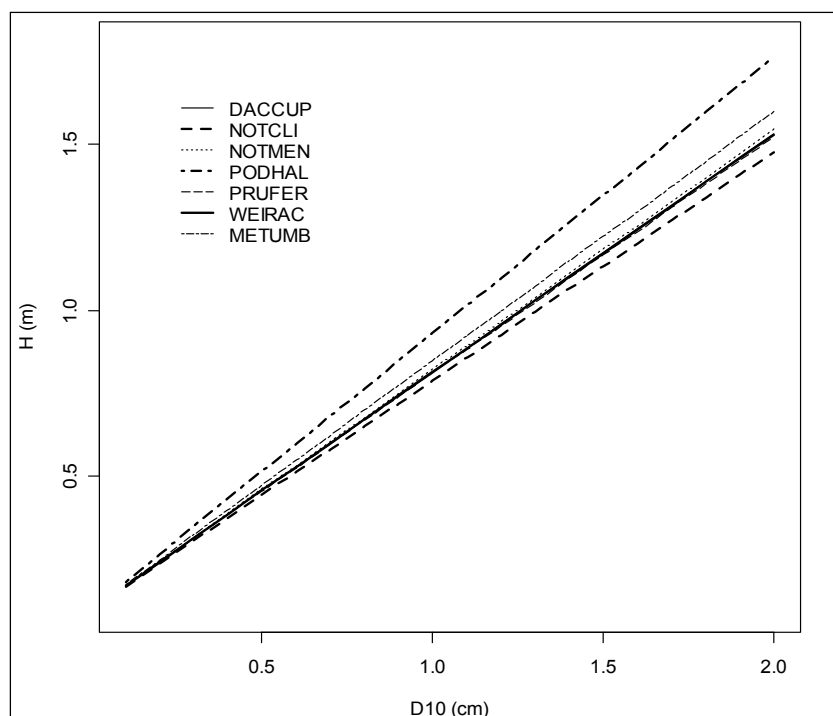
Figure 4 Allometric relationship between diameter at 10 cm (D_{10}) and height (H) for seedlings.

Table 2 Seedling allometry parameters. The number of seedlings sampled is shown (Repl. = Replicates).

Species	Repl.	*a*	*b*	R^2
DACCUP	1486	0.1	0.72	89.0
NOTCLI	1597	0.1	0.69	84.6
NOTMEN	2050	0.1	0.72	84.9
PODHAL	714	0.1	0.83	83.3
PRUFER	2172	0.1	0.71	88.0
WEIRAC	1388	0.1	0.71	77.8
METUMB	971	0.1	0.75	76.4

Sapling.—The relationship between height (*H*) and diameter (D_{10}) is represented by a power function (Figure 5):

$$H = a\, D_{10}^{\,b},$$

where *H* is the height of the sapling (m), D_{10} is the diameter at 10 cm height, and *a* and *b* are estimated parameters. We linearised the model by a log-log transformation. Height and diameter are both subject to natural variation and measurement error, thus we used Reduced Major Axis regression (RMA, a model II regression) to estimate the parameters, using the *s.slopes* function written for R (http://eeb37.biosci.arizona.edu/~brian/splus.html; see Isobe et al. 1990). Parameter estimates (Table 3) of the allometric diameter–height model for sapling species were based on saplings sampled in the Waitutu area for the estimation of a radial growth model (see Coomes et al. 2009). As for the sapling radial growth model, we use the parameter of DACCUP for METUMB.

Table 3 Sapling allometry parameters, for the relationship between height (*H*; m) and diameter at 10 cm (D_{10}; cm) for six species, as well as sample size (Repl.)

Species	*a*	*b*	Repl.
DACCUP	1.16	0.84	119
PODHAL	1.35	0.74	101
PRUFER	1.36	0.88	63
WEIRAC	1.70	0.75	76
NOTCLI	1.28	0.97	41
NOTMEN	1.52	0.81	80
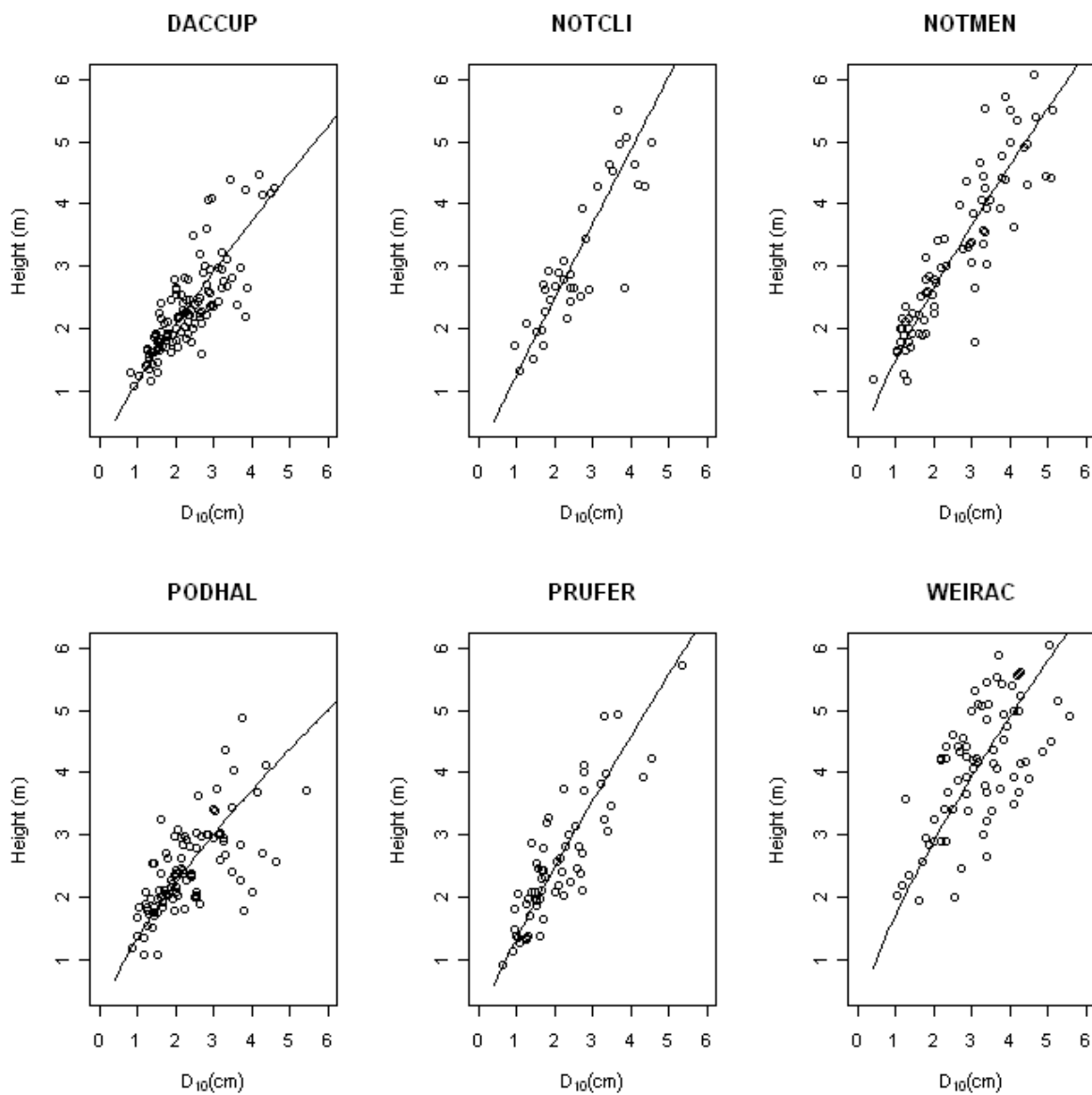
Figure 5 Allometric relationship between height (*H*) and diameter at 10 cm (D_{10}) for saplings.

The relationship between DBH and D_{10} (Table 4, Figure 6) was analysed as a linear model with Reduced Major Axis regression (RMA, a model II regression), based on the sapling data used in Coomes et al. (2009):

$$\text{DBH} = a + b\, D_{10}$$

Table 4 Sapling allometry parameters for the relationship between diameter at breast height (DBH at 1.35 m; cm) and diameter at 10 cm (D_{10}; cm), as well as sample size (Repl.)

	a	*b*	Repl.
DACCUP	−0.933	0.939	111
NOTCLI	−1.218	1.053	40
NOTMEN	−0.584	0.869	78
PODHAL	−0.551	0.815	96
PRUFER	−0.554	0.957	54
WEIRAC	−0.360	0.868	76
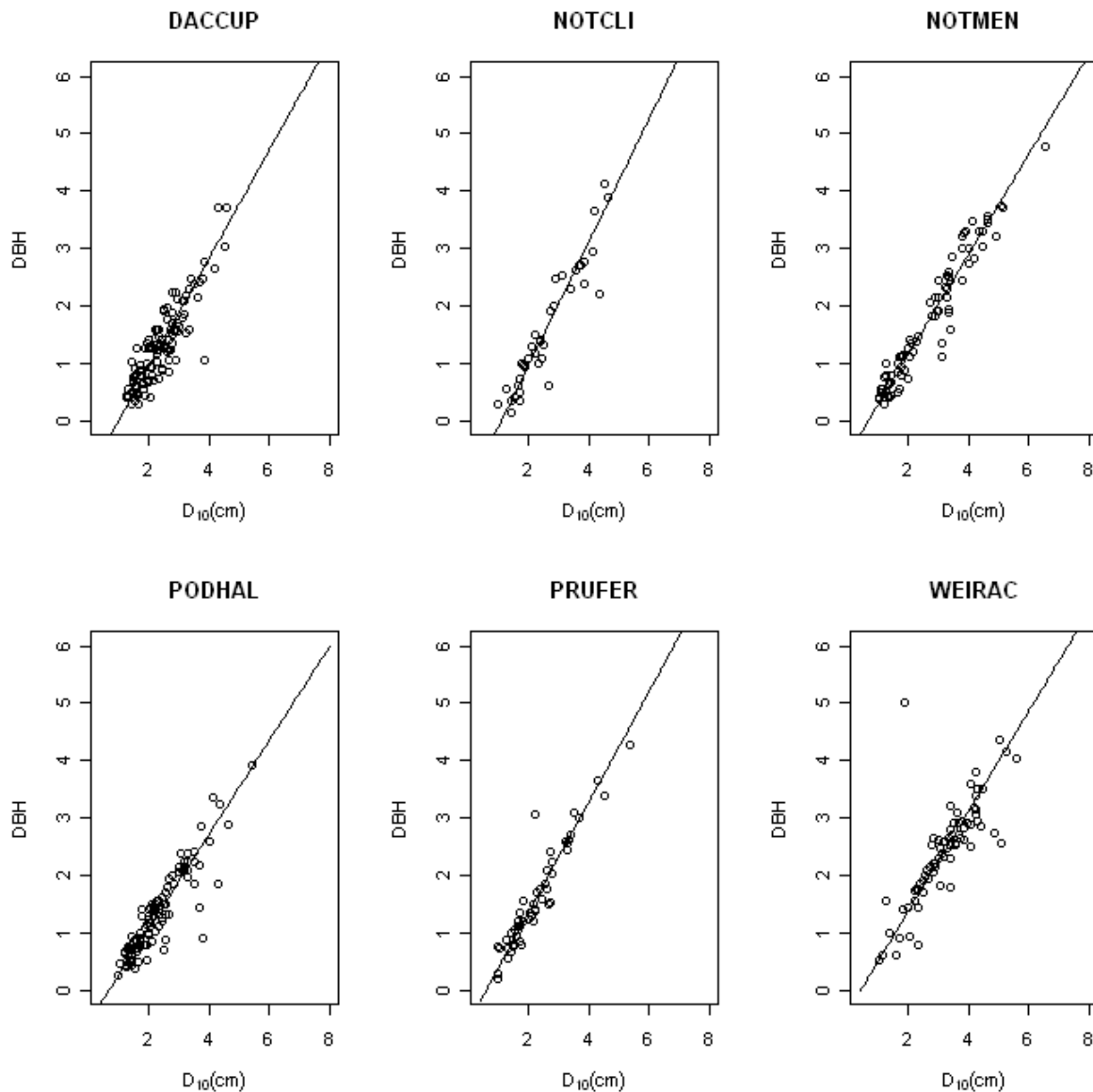
Figure 6 Relationship between diameter at breast height (DBH at 1.35 m; cm) and diameter at 10 cm (D_{10}; cm) for saplings.

Adult trees.—The data for adult-tree allometry were collected in mapped plots ranging from 1.4 to 2.25 ha located in Waitutu Forest (see Coomes et al. 2005). Trees were randomly selected within the plots. Tree height and crown height were measured using a Vertex hypsometer. The crown height is defined as the distance from the top of the tree to the base of the live crown. As in Canham et al. (1999) the base of the live crown was defined as the point where foliage occupied at least three of the four quadrants around the stem. As in Canham et al. (1999), the crown radius was measured by projecting the outermost margin of the crown on the ground, and taking the average of the two longest perpendicular radii. For each tree, DBH was also recorded.

The height–DBH–relationships (Table 5, Figure 7) were estimated according to the following equation for individuals with DBH > 0:

$$Height = 1.35 + (\text{maxht} - 1.35)(1 - e^{-b*DBH})$$

where maxht is maximum height of the tree.

Table 5 Adult-tree allometry parameters. Number of trees used for the estimation (Repl.) and R^2 of the regression

Species	Repl.	Maxht	b	R^2
DACCUP	70	25.28	0.054	0.886
METUMB	59	24.19	0.061	0.715
NOTCLI	34	30.13	0.041	0.702
NOTMEN	74	28.93	0.047	0.821
PODHAL	72	20.95	0.066	0.519
PRUFER	68	26.48	0.042	0.879
WEIRAC	130	18.26	0.088	0.686
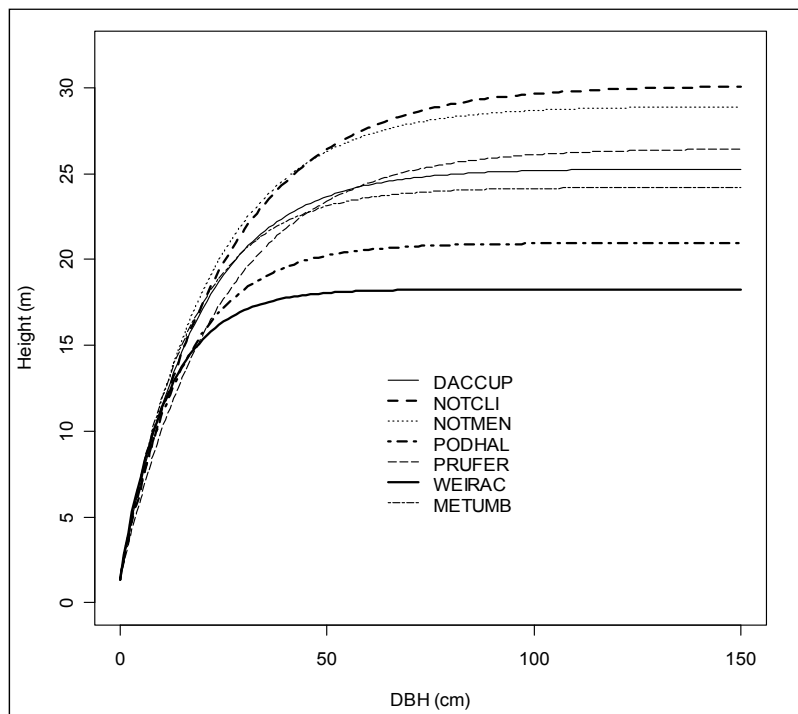
Figure 7 Height–DBH (diameter at breast height, 1.35 m) allometric relationships for adult trees.

The crown-height–height relationships (Table 6, Figure 8) were also estimated according to the following equation for trees with DBH > 0:

Crown height = $a \times$ height^b.

Table 6 Crown-height allometry parameters, number of trees used for the estimation (Repl.), and R^2 of the regression

Species	Repl.	*a*	*b*	R^2
DACCUP	68	0.078	1.54	0.67
METUMB	58	0.323	1.08	0.60
NOTCLI	34	0.339	1.03	0.65
NOTMEN	74	0.12	1.36	0.57
PODHAL	70	0.055	1.69	0.76
PRUFER	66	0.69	0.88	0.54
WEIRAC	63	0.364	1.11	0.65
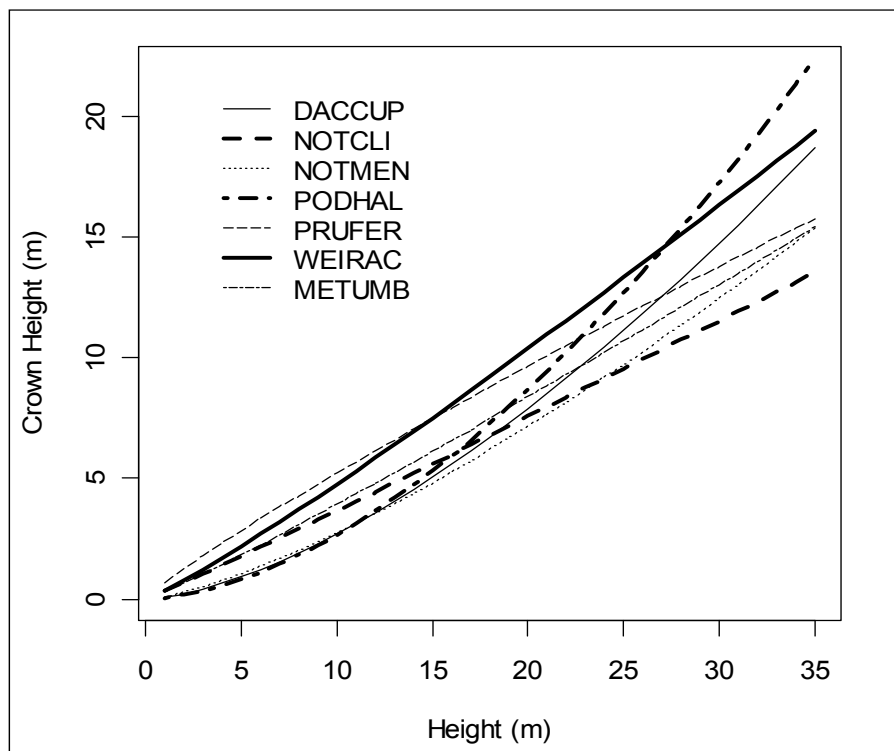
Figure 8 Crown-height–height allometric relationship for adult trees.

The crown-radius–DBH relationships (Table 7, Figure A9) were estimated, according to the following equation for trees with DBH > 0:

Crown radius = $a \times \text{DBH}^b$.

Table 7 Crown-radius allometry parameters, number of trees used for the estimation (Repl.) and R^2 of the regression

Species	Repl.	a	b	R^2
DACCUP	69	0.284	0.654	0.826
METUMB	58	0.353	0.583	0.718
NOTCLI	34	0.658	0.474	0.691
NOTMEN	74	0.388	0.634	0.862
PODHAL	72	0.411	0.532	0.743
PRUFER	68	0.553	0.534	0.718
WEIRAC	65	0.427	0.578	0.711
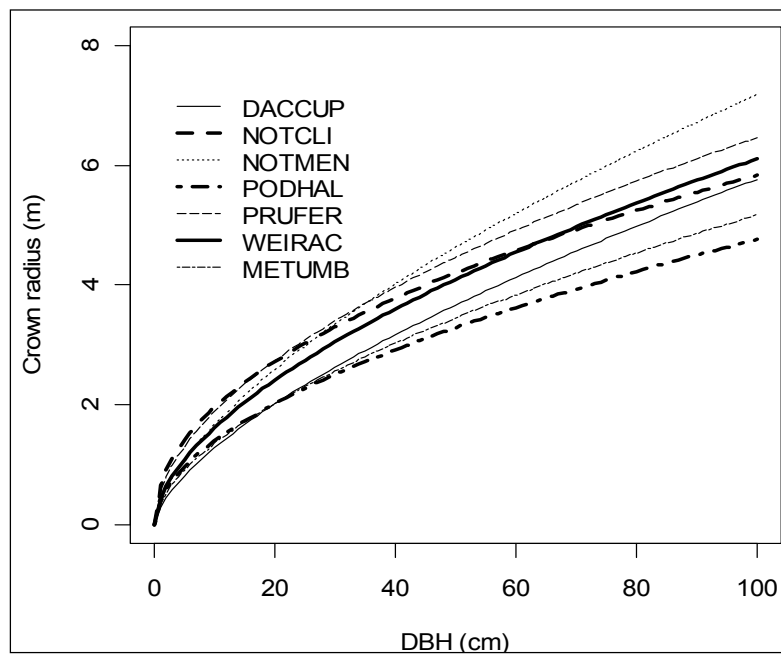
Figure 9 Crown-radius–DBH (diameter at breast height, 1.35 m) allometric relationship.

3.3 Modifications of crown-radius parameters used for the light model

In the field crown radius was measured as the maximum crown radius. In SORTIE the shape of the crown is represented by a cylinder, but for most of the tree species included in the model, the 'real' shape of the canopy is more similar to a spheroid or to a cone than a cylinder. Thus, as proposed by Canham et al. (1999), a rescaling factor was applied to the radius measured in the field to take account of difference between the field measurements and the cylindrical shape of the canopy in the SORTIE/NZ light-interception model.

The principle of the correction is to use a radius that would result in a cylindrical canopy volume that is the same as that volume measured in the field. The assumptions are that the canopies in the field are similar to a cone (or double cone), and that this cone is represented in SORTIE by a cylinder of the same volume. This results in rescaling the crown radius by sqrt(1/3) = 0.57. The modified parameters used in SORTIE for crown radii are thus given in Table 8. Figure 10 presents the different type of crown shapes and their corresponding volumes.

Table 8 Crown-radius allometry parameters from Table 7 rescaled by 0.57 for use in SORTIE/NZ

Species	*a*	*b*
DACCUP	0.161	0.654
METUMB	0.201	0.583
NOTCLI	0.375	0.474
NOTMEN	0.221	0.634
PODHAL	0.234	0.532
PRUFER	0.315	0.534
WEIRAC	0.243	0.578
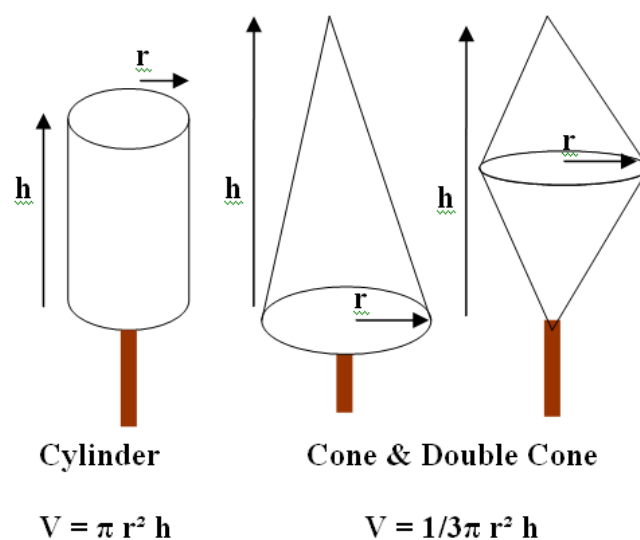
Figure 10 Different shapes of tree crowns and their volume (V).

4 Substrate behaviours

The substrate behaviours simulate the dynamics of the forest floor in which seeds germinate and grow into seedlings. The relative proportions of each kind of substrate are tracked in the substrate grid. The grid-cell resolution is set to 8 × 8 m. Within each cell, the grid keeps track of each substrate's area as a proportion of the total area. The quality of the substrate is taken into account in the recruitment behaviours, which estimate the probability of seedling establishment in each cell.

The substrate behaviour keeps track of five kinds of substrate:

- Tip-up mounds – mineral soil created by the uprooting of a tree
- Fresh logs
- Decayed logs
- Litter
- Moss

Litter and moss form a common substrate pool in fixed proportion to each other (see Figure 11). Fresh logs decay into decayed logs. Decayed logs and mineral soil decay into litter and moss. (If no new substrate was created, eventually the whole forest would be uniformly covered in litter and moss.) The creation of new substrates decreases the amount of litter and moss and starts the process over again. There is one way in which new substrates are added: tree fall. Tree fall allows SORTIE to account for small-scale dynamics by having some trees fall and create mineral soil and fresh logs. When a live tree dies, there is a certain probability that the tree will fall at death. For fallen trees, there is also a certain probability that the tree will expose an area of mineral-soil substrate.

Values of the substrate behaviour parameters for SORTIE/NZ were fixed based on expert knowledge, or set similar to the model SORTIE/BC (see Papaik & Canham 2006 and below). For decayed logs, quantitative data for *Nothofagus solandri* and *N. menziesii* show that logs take <100 years to decay to a soft, indistinguishable pulp. The parameters of the decay equation for species were set to result in the same decay rate (see Figure 12).
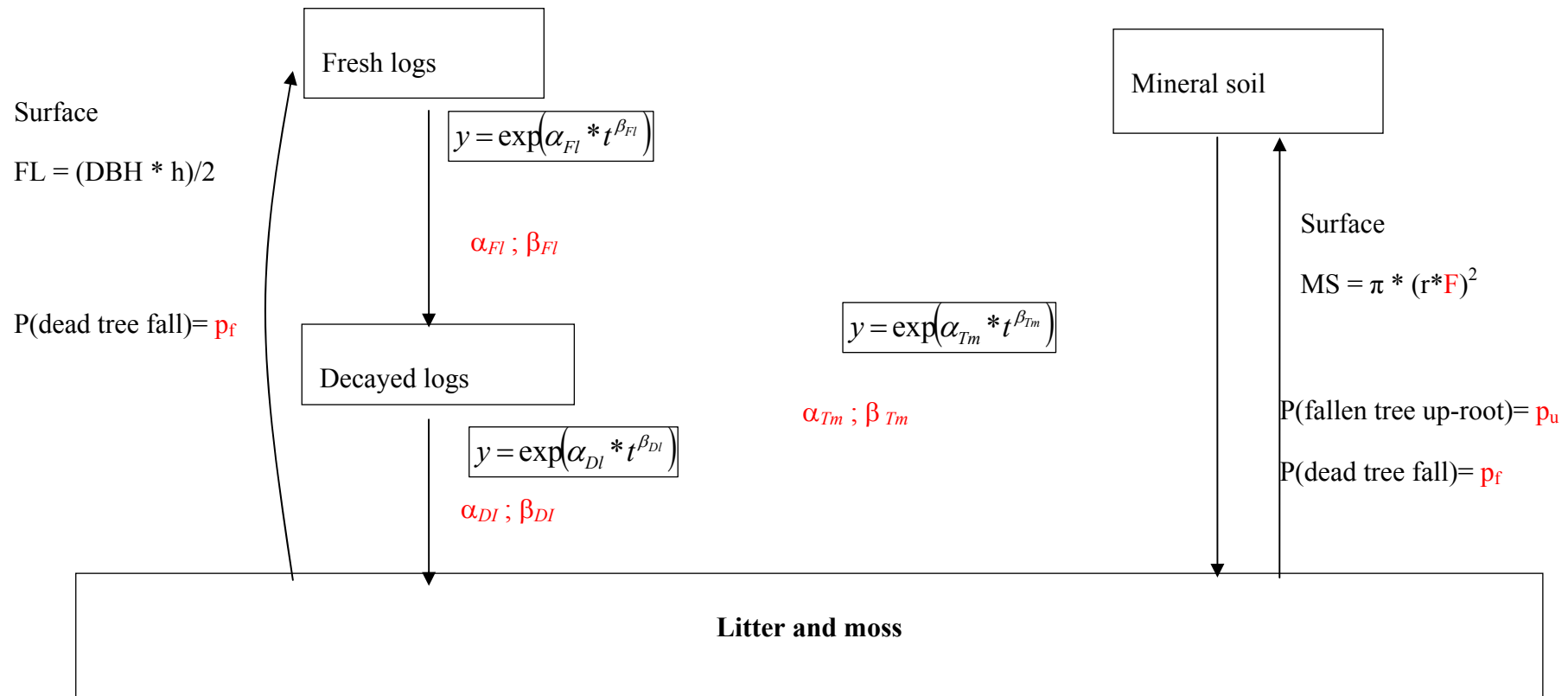
Figure 11 Description of the substrate behaviours and substrate parameters (in red).
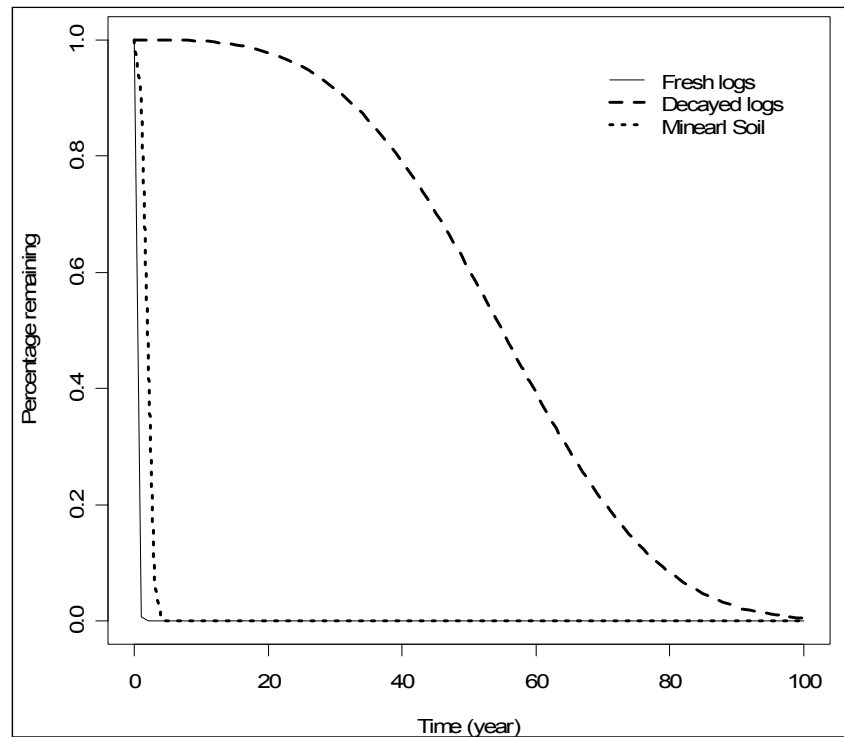
Figure 12 Decay function for three substrates: fresh logs, decayed logs and mineral soil.

Parameters of the substrate behaviours in SORTIE/NZ:

α_{Fl} The α exponent in the decay equation $y = e^{\alpha t\beta}$, applied to fresh logs (FL) = **−5**

β_{Fl} The β exponent in the decay equation $y = e^{\alpha t\beta}$, applied to fresh logs = **50,** this gives proportion of decayed logs in one year. Decayed logs are those with moss cover.

α_{Dl} The α exponent in the decay equation $y = e^{\alpha t\beta}$, applied to decayed logs = **−8.404888e-07**

β_{Dl} The β exponent in the decay equation $y = e^{\alpha t\beta}$, as applied to decayed logs = **3.4**

p_f The proportion of the total number of dead trees that fall each year, as a value between 0 and 1. This does not apply to snags = **0.15**

p_u The proportion of fallen trees that uproot to create new mineral soil substrate, as a value between 0 and 1 = **0.4**

α_{Tm} The α exponent in the decay equation $y = e^{\alpha t\beta}$, as applied to mineral soil = **−0.1**

β_{Tm} The β exponent in the decay equation $y = e^{\alpha t\beta}$, as applied to mineral soil = **3.0**

F The amount by which to multiply the tree's radius (r) when calculating the size of the new mineral soil (MS) exposed by fallen trees. This is meant to allow for the effects of roots = **4.1**

p_m The fixed proportion of the litter and moss pool that is moss. Expressed as a value between 0 and 1 = **0.73**

5   Recruitment behaviours

The parameters provided for recruitment are estimated using the density of seedlings in 1-m² quadrats established along transects in four mapped stands, and position and size of adult tree in the plots (see Lepage et al. (2000) for a more detailed description of the estimation method).

5.1   Study area

Permanent study plots of either 1.5 ha (East Crombie Marine (ECM), West Waitutu Marine (WWM)) or 2.25ha (East Waitutu Marine (EWM), West Crombie Marine (WCM)) were established in the austral summers of 2001/02 and 2002/03. The plots were placed in representative examples of the predominant vegetation type in alluvial and terraces sites (Coomes et al. 2005). Stems > 10-cm DBH of all canopy species and > 2.5-cm DBH of all subcanopy species in each plot were mapped from control points using an Impulse laser rangerfinder with digital inclinometer and compass (Laser Technology Inc., Colorado, USA).

Seedling data were collected from 4–8 permanent transects established in each of the four sites. Transects were composed of adjacent, 1-m² quadrats, for a total of 318–330 quadrats per site. The position of each transect was established using randomly selected starting points, but with the condition that the transect remained a minimum of 30 m from the nearest plot edge. The spatial position of each quadrat was mapped from control points, using an Impluse500 laser rangefinder with a digital inclinometer and compass (Laser Technology Inc., Colorado, USA). Seedlings were censused during the summers of 2001 (ECM and WWM sites) and 2002 (EWM, and WCM sites). The number of seedlings (in height class 5–15 cm), substrate type (see later for definition of substrate type) and species were recorded in each quadrat.

5.2   Dispersal behaviour

Dispersal behaviours create and distribute tree seedling around modelled stands. In SORTIE/NZ, two dispersal functions are used (Table 9), either a Weibull function (Table 10), or a lognormal function (Table 11). Seedling density varies according to distance from the parent tree (Figure 13).

Table 9 Dispersal functions for species

	Function
DACCUP	Lognormal
METUMB	Lognormal
NOTCLI	Weibull
NOTMEN	Lognormal
PODHAL	Lognormal
PRUFER	Weibull
WEIRAC	Weibull

1. Weibull function

$$R_i = STR \sum_{j=1}^{n} \left(\left(\frac{DBH_j}{30} \right)^{\beta} e^{-Dd_{ji}^{\theta}} \right)$$

where:

R_i is the density (#/m^2) of seedlings at a given point i

STR, the 'standardised total recruits', is the potential number of seedlings produced by a 30-cm-DBH parent tree

DBH_j is the DBH (cm) of the $j = 1...T$ parent trees within a specified radius of location i

D is a species-specific dispersal parameter

d_{ji} is the distance (in metres) from point i to the jth parent tree

θ and β are dispersal parameters

Table 10 Weibull dispersal parameters for three species

	STR max.	Normaliser	DBH min.	β	D	ϑ
NOTCLI	457.505	470.11	6.90	0.624	778.37	1.13
PRUFER	967.201	2140.92	9.42	2.803	541.74	1.00
WEIRAC	182.175	1880.13	2.50	0	289.27	1.18

In SORTIE D is divided by 10 000.

2. Lognormal function

$$R_i = STR \sum_{j=1}^{n} \left(\left(\frac{DBH_j}{30} \right)^{\beta} e^{-\frac{1}{2} \left(\frac{\left(\ln \left(d_{ij}/X_0 \right) \right)^2}{X_b} \right)} \right)$$

where:

R_i is the density (#/m^2) of seedlings at a given point i

STR, the 'standardised total recruits', is the number of seedling recruits produced by a 30-cm-DBH parent tree

DBH_j is the DBH (cm) of the $j = 1...T$ parent trees within a specified radius of location i

d_{ij} is the distance (in meters) from point i to the jth parent tree

X_0 is the mean of the function

X_b is the variance of the function

β is a dispersal parameter

Table 11 Lognormal dispersal parameters (see definitions above) for four species

	STR max.	Normaliser	DBH min.	β	X_o	X_b
DACCUP	217.26	87430.29	10.54	2.6	44.54	0.81
METUMB	538.13	1004.21	2.58	3.15	0.21	1.87
NOTMEN	50.89	4403.37	18.11	5	4.22	1.15
PODHAL	216.73	1166.74	2.54	0	0.19	1.92
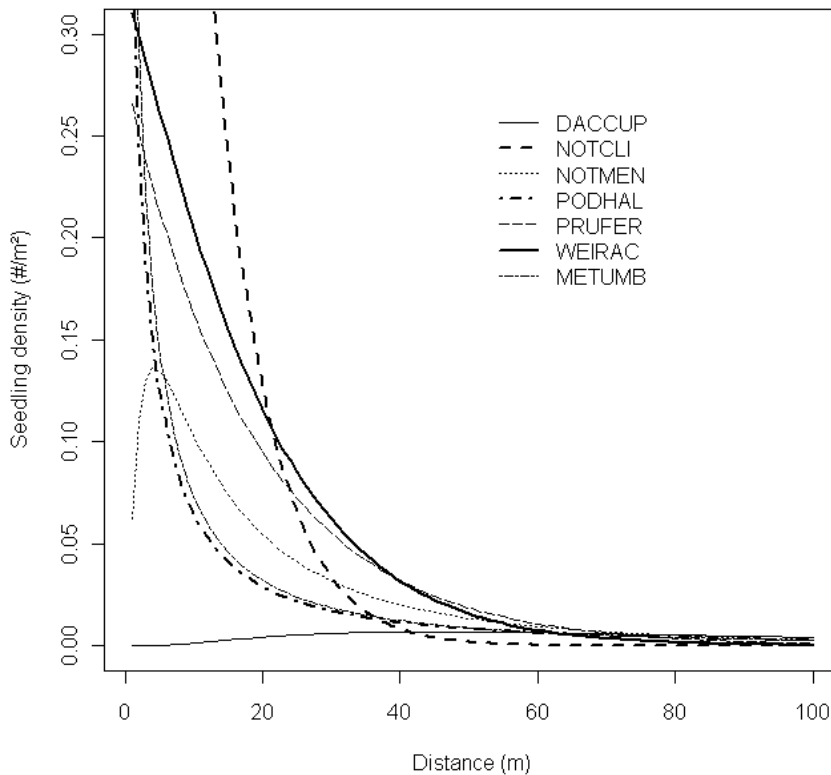
Figure 13 Seedling density as a function of the distance from a tree (of DBH = 30 cm). This graph is for the substrate with the best establishment rate (i.e. = 1) and for an STR (standardised total recruits) set to 600 for all species.

5.3 Tree fecundity

The minimum DBH for reproduction is set to 10 cm. To avoid excessive differences in fecundity between species for large-diametered trees we set the scaling parameter of the fecundity $\beta = 2$ for all the species. The dispersal estimations provide a field estimation of the fecundity parameters (*STR*). However, these values are based on point-in-time existing seedling counts and do not represent the enormous temporal variability in tree seed production. The number of seedlings between 5 and 15 cm in height is a function of not just the annual production of seedlings but also seedling growth and survival. We have thus decided, as in the original SORTIE (Pacala et al. 1996), to set *STR* as identical for all the species. We completed runs involving different values for *STR* and we selected the value that yielded to densities of small seedling (< 20 cm in height) most consistent with field data and resulting in minimum computation time: *STR* = 0.5 for all species.

5.4 Establishment behaviour

Light effect and density dependence.—There was no evidence for light or density-dependence effects on recruitment and so no light or density-dependence effects were included in SORTIE/NZ.

Substrate favourability.—Establishment behaviour takes the substrate composition of each grid cell in the substrate grid and converts it into a single number for each species, called the 'substrate favourability index'. The favourability index is the sum of the proportions of each substrate multiplied by the favourability of that substrate. This index represents the proportion of total seeds of that species that are expected to survive in that grid cell of a stand. The substrate favourability indexes were estimated together with the dispersal model (Table 12, Figure 14).

Table 12 Substrate favourability parameters for the seven species used in SORTIE/NZ

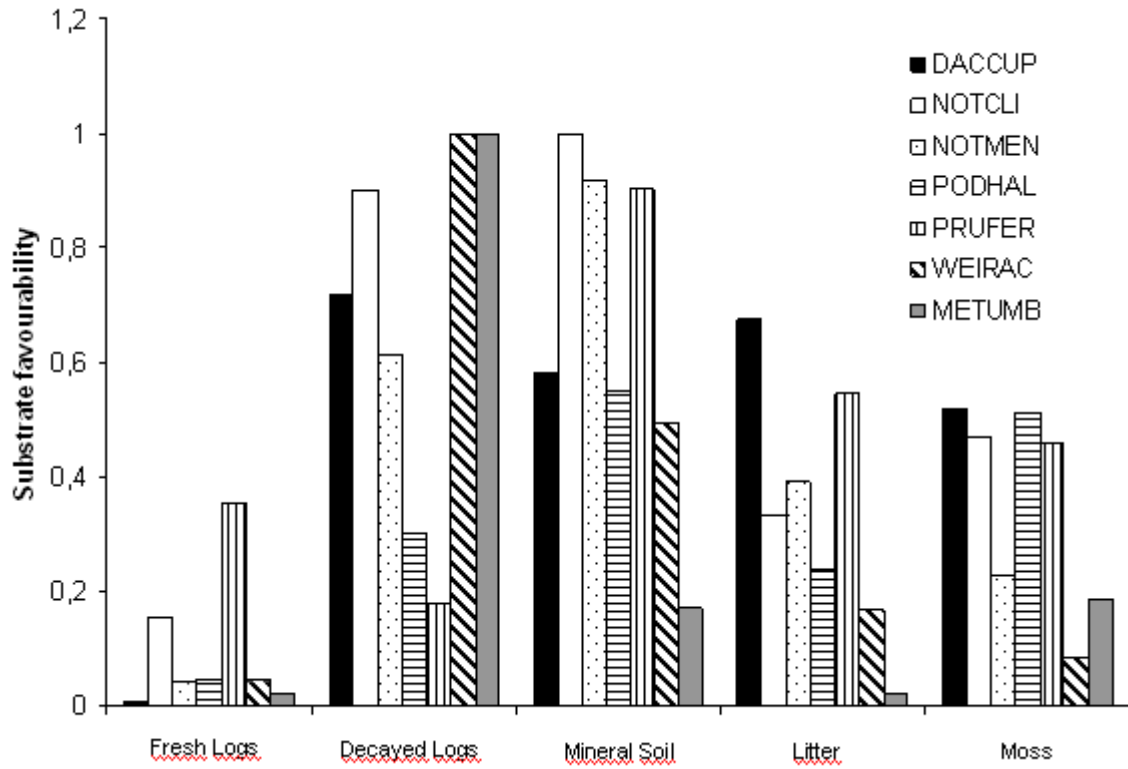|	DACCUP	NOTCLI	NOTMEN	PODHAL	PRUFER	WEIRAC	METUMB
Fresh logs	0.0073	0.1529	0.0425	0.0482	0.3559	0.0436	0.0217
Decayed logs	0.7181	0.8999	0.6150	0.3007	0.1799	1	1
Mineral soil	0.5823	1	0.9165	0.5492	0.9043	0.4940	0.1690
Litter	0.6733	0.3325	0.3927	0.2392	0.5447	0.1683	0.0205
Moss	0.5185	0.4709	0.2273	0.5125	0.4599	0.0845	0.1866

Figure 14 Substrate favourability for the seven species used in SORTIE/NZ.

6 Growth behaviours

6.1 Seedling growth

In February–March 2003, 1-m^2 quadrats were established in patches of seedlings on the forest floor (see Kunstler et al. 2009). The quadrats were distributed in sufficient numbers to include approximately 1000 seedlings for each of the seven species, and were stratified across a range of light levels and substrate types. Each seedling was identified by species, and a mark of white paint was made on the stem 2 cm above the root collar. Seedling heights were measured as the stretched distance from the painted mark to the apical bud. All seedlings were subsequently resurveyed in January 2005, with each seedling being recorded as either alive or dead. Heights were also remeasured on the living seedlings. These data were used to analyse seedling height growth in relation to height and light availability (using a quantum sensor; Table 13, Figure 15).

The Michaelis–Menten equation was used to model annual height growth for each tree species:

$$\frac{dH}{dt} = \frac{\alpha L}{(L + \alpha / \beta)} H^{\phi}$$,

where *H* is the height (cm) of the seedling, *L* is the light available for the seedling (0–100% of daylight), *α* and *β* are parameters describing the asymptotic growth in high light and the slope of the function at zero light, respectively, and *ϕ* is a parameter that describes the changes in growth rate with size. The growth model was estimated for seedlings that lacked any sign of damage by deer. See Kunstler et al. (2009) for details.

Table 13 Parameter estimates for each tree species for a model with the height growth for seedling in cm/year. Number of seedlings remeasured on the marine terrace site at Waitutu Forest, Southland (Repl.)

Species	*α*	*β*	*Φ*	Repl.
DACCUP	0.56	0.21	0.351	1334
NOTCLI	1.05	3.29	0.014	1598
NOTMEN	0.65	36.16	0.189	1005
PODHAL	0.32	1.811	0.404	729
PRUFER	0.63	99.79	2.6E-12	1609
WEIRAC	0.75	82.15	2.7E-85	782
METUMB	1.11	0.42	0.0263	974
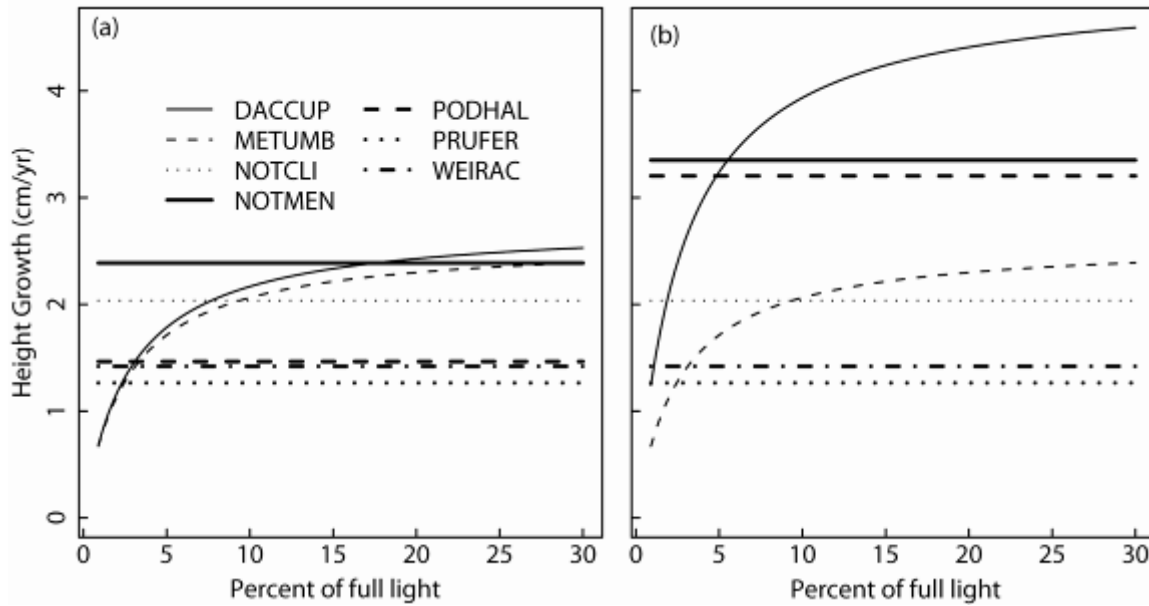
Figure 15 Predicted height growth as a function of percent full light for seedlings (a) 15 cm or (b) 50 cm in height, growing on the terrace sites at Waitutu Forest, Southland.

6.2   Sapling growth

Saplings were individuals taller than 1.35 m in height and up to 10-cm DBH. The growth function was estimated with radial growth data of saplings. For each individual, light availability (using a quantum sensor) was measured (Coomes et al. 2009). The growth model was estimated with a Michaelis–Menten function for the effect of light, and a power function for the effect of size. Then α and β were recalculated to predict the diameter growth in cm/year (and not mm/year as in Coomes et al. (2009)) and to use a D_{10} in centimetres (and not in millimetres as in Coomes et al. (2009)) (see Table 14 and Figure 16).

The diameter growth of saplings is determined by a Michaelis–Menten function for the effect of light:

$$G = \frac{\alpha L}{(L + \alpha / \beta)} D_{10}^{\phi},$$

where G is diameter growth (cm/year), D_{10} is stem diameter at 10 cm height (cm), L is light availability (0–100% of daylight), α, β, and φ are estimated parameters. α is the asymptotic growth at high resource level, β is the slope of the function at zero light. Functions were estimated using *gnlr* R package *gnlm* (the *gnlr* routine in the *gnlm* R package of Dr Jim Lindsey and downloaded from http://popgen0146uns50.unimaas.nl/~jlindsey/rcode.html) see Coomes et al. (2009). After preliminary exploration of the dataset, we set error to be normally distributed, with a mean of zero, and variance that varied as a linear function of the predicted mean.

Table 14 Parameter estimates for each of seven dominant tree species at Waitutu, Southland used in the SORTIE/NZ model. Number of saplings sampled (Repl.)

Species	α	β	ϕ	R^2	Repl.
DACCUP	0.031	0.0124	0.55	0.57	54
NOTCLI	0.069	0.0060	0.55	0.15	39
NOTMEN	0.036	0.0099	0.55	0.66	40
PODHAL	0.024	0.0259	0.55	0.53	57
PRUFER	0.029	0.0088	0.55	0.35	54
WEIRAC	0.025	0.0301	0.55	0.28	49
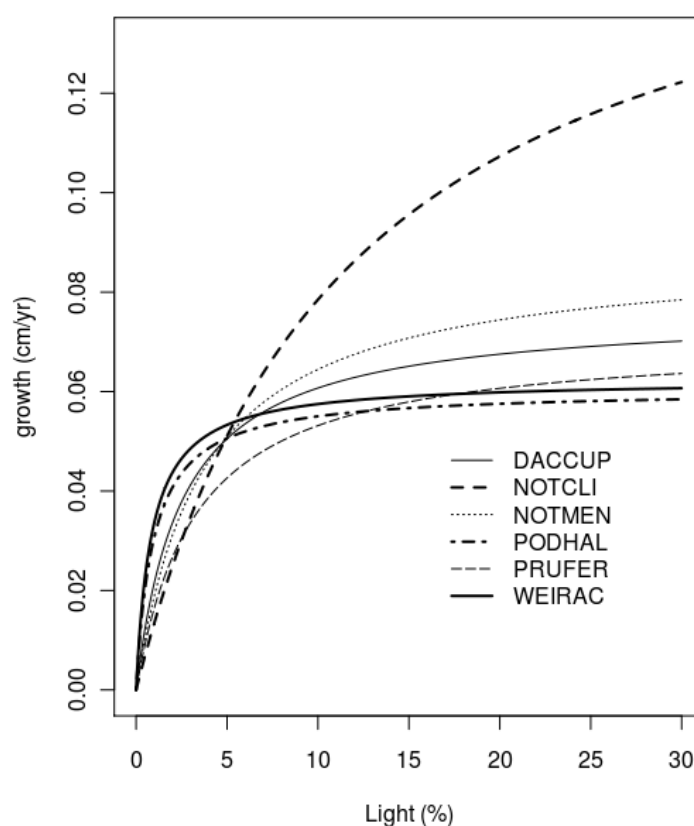
Figure 16 Predicted diameter growth as function of light for a sapling of D_{10} = 5 cm.

6.3 Adult growth

An analysis of tree growth was made using NVS Databank permanent plots in Southland of <600 m elevation. We set this upper elevation limit in order to keep plots with similar climates to Waitutu Forest.

Description of the data used.—520 NVS plots (20 × 20 m plots were used in these analyses) that have been measured at least two times between 1970 and 1997, and in which each tree was tagged and DBH measured. We used trees with DBH > 10 cm.

Table 15 Description of the growth dataset. Number of adult trees used in the estimation is given (Repl.)

	Repl.	Mean growth (mm/year)	Mean diam. (cm)
DACCUP	1157	1.07	38.8
METUMB	823	1.14	37.3
NOTCLI	716	2.22	26.5
NOTMEN	921	2.17	37.0
PODHAL	490	0.49	26.0
PRUFER	452	1.11	29.4
WEIRAC	5963	1.11	21.1

*Growth equation.—*We decided to use a simplification of the Neighbourhood Competition Index (NCI) growth equation of Canham et al. (2004), which is the following growth model (Table 16):

Growth = Max growth × Size effect × Crowding effect,

with Max growth as the maximum growth that a tree can attain;

Size effect:

$$SE = e^{-1/2\left(\frac{\ln\left(DBH/X_0\right)}{X_b}\right)^2}$$; and

Crowding effect:

$$CE = e^{-C\times\left(BA\sup_p/1000\right)^D},$$

with $BA\sup_p$ the basal area of trees bigger than the target tree (Sum(Pi*(DBH/2)²) for DBH > DBH target tree), and X_0, X_b, C and D estimated parameters. The plot area is 400 m² (20 × 20 m). In SORTIE/NZ we compute the basal area of trees within a radius of 11.28 m around the target tree (400 m²). Models with either no competition effect or with competition effect $BA\sup$ were tested.

Table 16 Parameters limits used in the likelihood estimation for tree growth

Parameters	Lower boundary	Upper boundary
Max growth (MaxG)	0	30
X_0	1.5	600
X_b	0	50

Table 17 Parameters estimated for the best adult growth model and AICc (Akaike Information Criteria corrected for small sample size) of the model with no basal area effect (*No BA*) or with a basal area of tree bigger than the target tree effect (BA_{sup})

	MaxG	X_0	X_b	C	D	R^2	AICc *No BA*	AICc BA_{sup}
DACCUP	1.52	571.2	3.56	4.69E-04	1.43911	0.0229	3337.9	3340.4
METUMB	4.05	599.9	1.96	0.224	1.00E-03	0.0884	3298.4	3298.4
NOTCLI	2.87	75.1	1.73	3.21E-31	3.09014	0.0483	2953.9	2958.0
NOTMEN	2.74	73.9	1.81	4.85E-02	0.00123	0.0390	3837.7	3841.7
PODHAL	1.46	36.2	1.58	0.747	0.09623	0.0516	845.2	829.7
PRUFER	2.20	251.6	3.31	0.160	0.37267	0.0384	1453.3	1451.4
WEIRAC	3.92	600	2.60	0.152	0.31318	0.0644	18903.8	18855.0

For some species the best model does not include a *BA* competition effect (Table 17), but it is simpler to use the same function for all the species, given that for these species the effect of competition on growth is nil (see Figure 17).
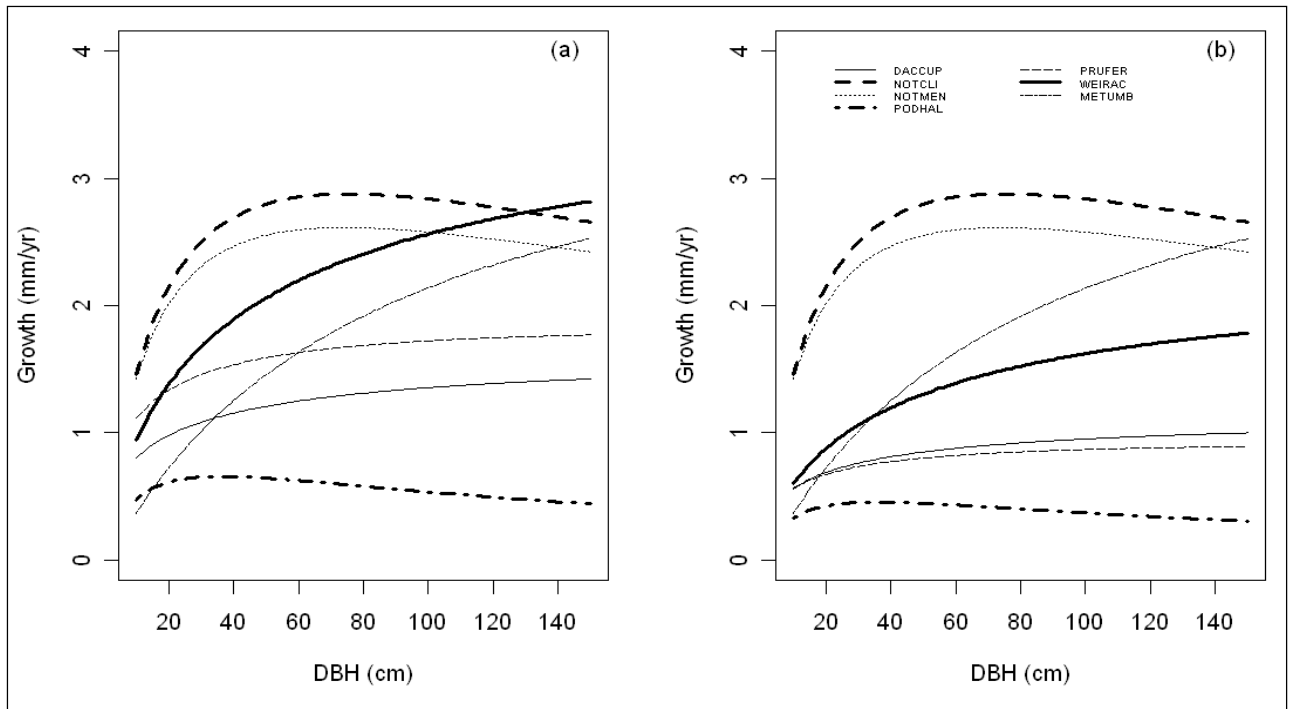
Figure 17 Diameter growth of the seven species as a function of DBH from 10 cm to 150 cm trees (a) no local competition (*BA*sup, the basal area of the trees bigger than the target tree set to 0 cm²) and (b) high local competition (*BA*sup set to 100 cm²).

7   Mortality behaviours

7.1   Seedling mortality

The seedlings tagged for growth behaviours were subsequently resurveyed, with each seedling being recorded as either alive or dead. A survival model with a light effect (measured with quantum sensor) and a size effect was estimated using maximum likelihood (Table 18).

Table 18 Description of the seedling survival dataset. Initial number of living seedlings used in the estimation is given (Repl.)

| Species	Repl.	Min. size (cm)	Max. size (cm)	Min. light (%)	Max. light (%)
DACCUP	1486	0.65	96	0.96	27.59
METUMB	971	0.45	36.2	0.96	23.42
NOTCLI	1596	0.45	48.9	0.87	27.59
NOTMEN	2050	0.41	68.5	2.02	21.46
PODHAL	714	0.12	92.2	2.15	19.69
PRUFER	2172	0.61	75	0.87	23.42
WEIRAC	1388	0.4	52	0.87	23.42

The model estimated the annual probability of mortality, given by $p(H,L)$:

$$p\left(H,\,L\right) = M_{\max}\ e^{-a \times H^{\,b} - c \times L^{\,d}}\ ,$$

with H the height of the seedling (m) and L the percentage of light available for the seedling (Table 19, Figure 18).

<div align="center">

Table 19 Parameters estimated for the seedling survival model

</div>

	$M_{\max}$	a	b	c	d
DACCUP	0.998	7.21	0.387	3.76E-14	9.82
METUMB	0.999	9.54	0.498	2.31E-11	10
NOTCLI	0.983	2.04	0.196	5.26E-06	4.10
NOTMEN	0.284	20	1.845	8.03E-06	3.84
PODHAL	1	20	0.727	0.00017	3.36
PRUFER	0.996	3.47	0.230	3.02E-05	3.65
WEIRAC	0.974	20	1.544	1.293	6.84E-15
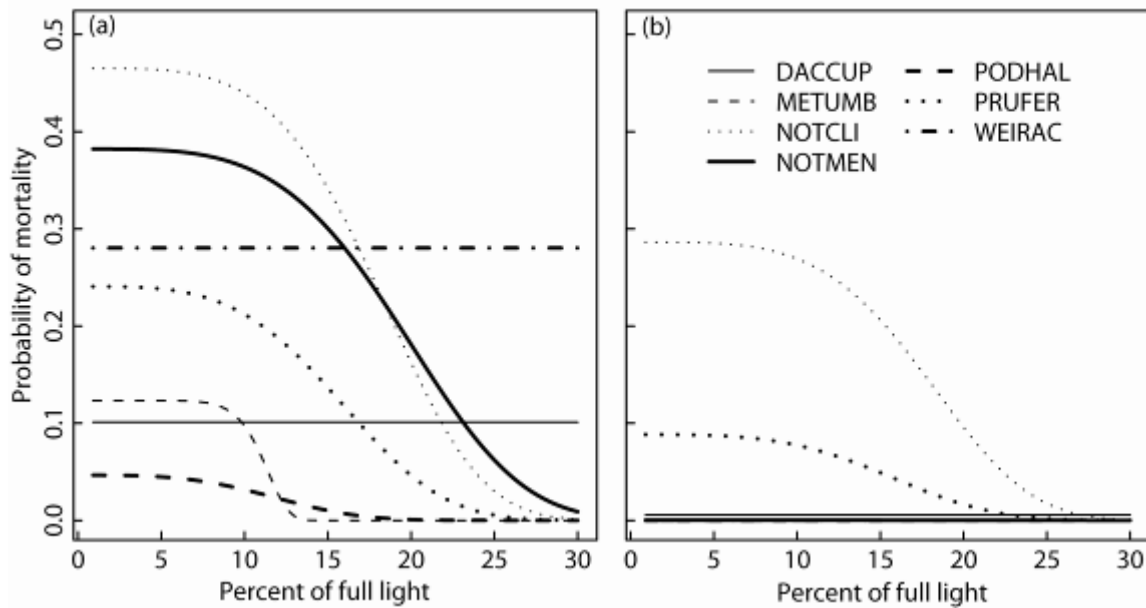
Figure 18 Predicted probability of mortality as a function of percent of full light for seedlings (a) 15 cm or (b) 50 cm in height, growing on the terrace sites at Waitutu, Southland.

7.2 Sapling mortality

Based on the NVS plots used for adult trees (see the following section 'Adult mortality' for a description of the dataset), we have estimated a mean annual mortality rate for trees with DBH < 10 cm (Table 20).

Table 20 Parameters estimates for sapling annual probability of mortality. The number of saplings sampled is shown (Repl.)

	Repl.	Probability of mortality
DACCUP	388	0.0058
METUMB	135	0.0095
NOTCLI	475	0.0104
NOTMEN	476	0.0136
PODHAL	334	0.0063
PRUFER	116	0.0091
WEIRAC	4730	0.0108

7.3 Juvenile density-dependent mortality

Our calibration lacked data to properly evaluate the density-dependent mortality for saplings and large seedlings. Indeed the sapling dataset does not provide light measurements with which to estimate how sapling mortality was affected by light. For the seedlings the bulk of the dataset was smaller than 50 cm in height, thus precluding a robust estimation of the light

effect for large seedlings. Preliminary long-term simulation (2000 years) revealed that because of this weak density-dependent mortality the model failed to regulate juvenile populations, resulting in unrealistically high densities of juveniles in closed forests. This increased computation time too much. We thus decided to add an additional mortality function, directly including density-dependent mortality in the same way to each species.

For each seedling and sapling, when the density of neighbouring seedlings and saplings within a 5-m radius is greater than a threshold value (*minimum density for mortality*), the mortality rate was increased using the following equation:

$$p(density, diam_m) = \frac{(A + C * diam_m) * density}{\frac{(A + C * diam_m)}{S} + density},$$

where *density* is the density of neighbouring seedlings and saplings within a 5-m radius, and *diam_m* is the mean diameter (cm) of neighbours measured 10 cm above root collar. *A*, *C*, and *S* are parameters respectively representing an asymptote of probability of mortality, mean diameter effect and density effect.

We ran several simulations involving different values of the parameters *minimum density for mortality*, *A*, *C*, and *S* and selected the parameter values that yielded densities of seedlings and saplings most consistent with field data (*minimum density for mortality* = 4000 stems/ha, *A* = 0.7, *C* = 0.04, and *S* = 0.000075). This addition of mortality does not modify the species hierarchy in terms of the mortality rate estimated with the field data.

7.4   Adult mortality

In this section the results of an analysis of tree survival from 560 NVS permanent plots (elevation < 600 m; Wiser et al. 2001) are presented based on being remeasured at least two times between 1969 and 2004 (Table 21, Figure 19). In each plot, trees were tagged and DBH measured (520 plots are 20 × 20 m square and the remaining plots are of varying size – mostly circular plots). This analysis is based on trees with a DBH > 10 cm.

Survival equations.—The annual survival model is a simplification of the NCI survival equation of Canham et al. (2004). The equation is similar to the growth model:

Probability of survival = Max.s × Size effect,

with Max.s the maximum survival that a tree can attain;

Size effect:

$$SE = e^{-1/2\left(\frac{\ln(DBH/X_0)}{X_b}\right)^2},$$

with X_0 and X_b as estimated parameters.

Table 21 Parameters for the adult-tree survival model. The number of adult trees used for the estimation is shown (Repl.)

	Repl.	Max.s	X_0	X_b
DACCUP	1310	0.9987	51.76	14.40
NOTCLI	1122	0.9906	22.90	9.60
NOTMEN	1353	0.9954	35.38	11.27
PODHAL	697	0.9953	16.93	11.62
PRUFER	558	0.9938	24.83	7.80
WEIRAC	7529	0.9945	21.85	9.63
METUMB	1079	0.9980	193.73	23.80
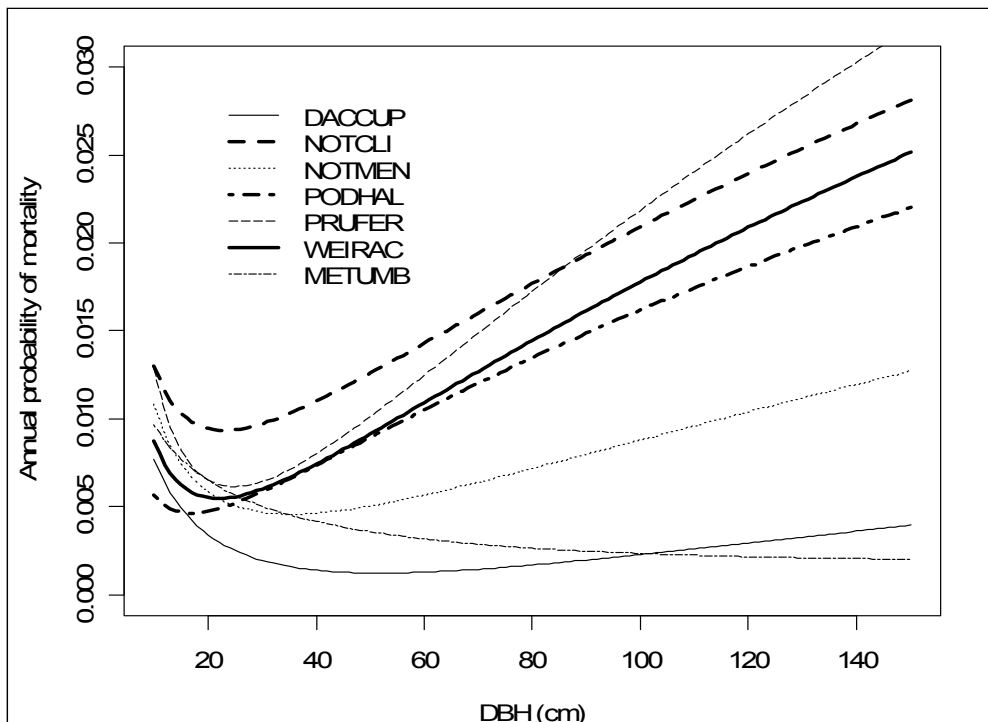
Figure 19 Annual probability of mortality of adult trees as a function of the DBH (diameter at breast height, 1.35 m).

Preliminary simulations revealed that a slightly too low adult mortality resulted in unrealistically large basal-area predictions. We thus decided to include a constant mortality rate in addition to this size-dependent equation similarly for all species. We ran several simulations adding different values of mortality and selected the value that yielded predictions of realistic basal area in monoculture (addition of 0.15% of annual mortality to all species). The addition of this mortality value does not modify the species hierarchy in terms of mortality rate estimated with field data.

7.5   Senescence mortality

This behaviour is meant to slightly increase the death rate among large adult trees and thus avoid simulating the growth of a tree up to an unrealistic size (e.g. 20-m DBH). Given the very slow growth of the trees in Waitutu Forest this was not a major issue. Only DACCUP was able to produce an unrealistically large tree. We set the parameters to increase the probability of mortality for trees bigger than the maximum DBH observed in Waitutu Forest, plus 20% (Table 22).

Table 22 Maximum DBH (diameter at breast height, 1.35 m) observed in the mapped plots and the maximum DBH limit set in SORTIE/NZ (maximum DBH plus 20%)

| SPECIES	Max DBH	Senescence limit
DACCUP	112.0	134.0
METUMB	130.0	156.0
NOTCLI	100.0	120.0
NOTMEN	120.0	144.0
PODHAL	100.0	120.0
PRUFER	100.0	120.0
WEIRAC	100.0	120.0

The senescence function is:

$$m_s = \frac{e^{(\alpha + \beta(DBH - DBH_s))}}{1 + e^{(\alpha + \beta(DBH - DBH_s))}},$$

where m_s is the probability of mortality and the parameters are senescence mortality, α, senescence mortality, β (= 0.06), and DBH at onset of senescence (DBH_s), in centimetres: DBH_l (= 00) (Table 23, Figure 20).

Table 23 Parameters of the senescence mortality function

| SPECIES	α	β	DBH_l
DACCUP	−4.836	0.06	100
NOTCLI	−3.972	0.06	100
NOTMEN	−5.412	0.06	100
PODHAL	−3.972	0.06	100
PRUFER	−3.972	0.06	100
WEIRAC	−3.972	0.06	100
METUMB	−6.132	0.06	100
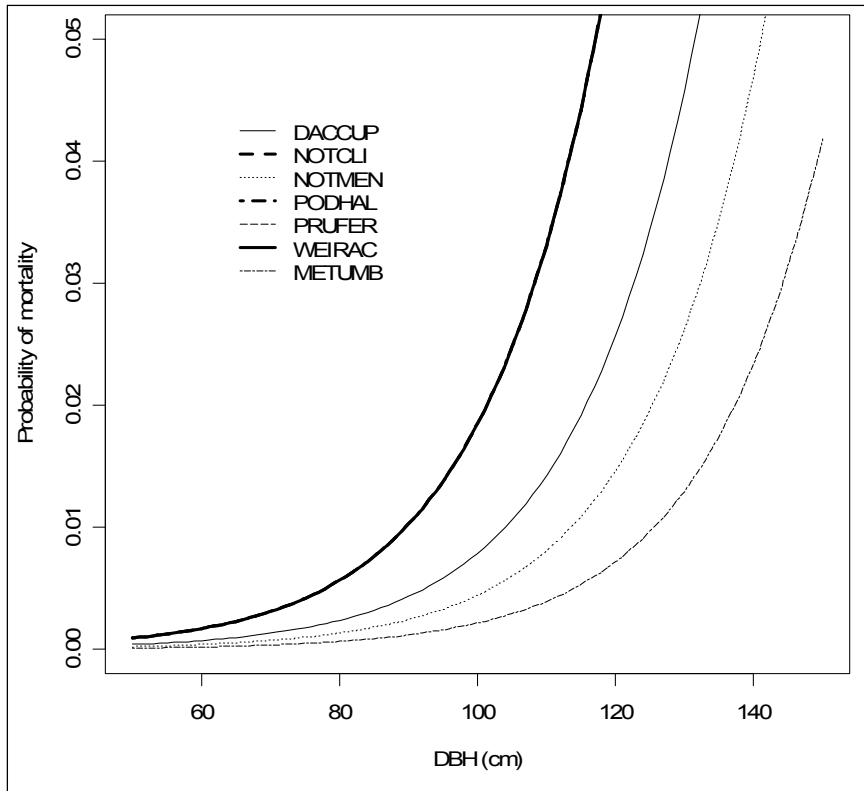
Figure 20 Probability of mortality as a function of DBH (diameter at breast height, 1.35 m) for the senescence behaviour (NOTCLI, PODHAL, PRUFER, and WEIRAC have the same curve).

8 Light behaviours

8.1 GLI light and quadrat GLI light

The light behaviour submodel computes a global light index (GLI), which measures the whole-season photosynthetically active radiation similarly to field estimates of light availability with hemispherical photos (Canham et al. 1999). GLI is computed for grid cells (quadrat GLI behaviour) or saplings and tree (GLI light behaviour) as a function of the crown geometry of each species, locality, size and identity of trees in the neighbourhood, and the species-specific light transmission coefficients. The crown of the tree is represented as a cylinder of radius and height given by the allometric equation (Figure 21). The parameters for species light transmission were estimated using images of individual tree canopies following the method of Canham et al. (1999). The general method consists of taking fish-eye-lens photographs in locations where either a significant proportion or the entire crown of an identified individual is visible. The crown is delineated in the photograph. The fish-eye-lens photographs were taken following standard procedure at 135 cm height and oriented to magnetic North (by S. Richardson, P. Bellingham and analysed by C. Morse). Then the percentage of canopy openness was analysed for individual circular sections of the canopy using the GLA software 'registration tool' (http://www.ecostudies.org/gla/). (See Figure 22 for an example of an image analysed with GLA software.) The parameters for species' light transmission are then set to the mean canopy openness of the species.

We report here the values of parameters estimated (Table 24). The values for canopy close to the forest floor (angle between forest floor and centre of the canopy <40°) were excluded because they do not allow a good estimation of canopy openness.
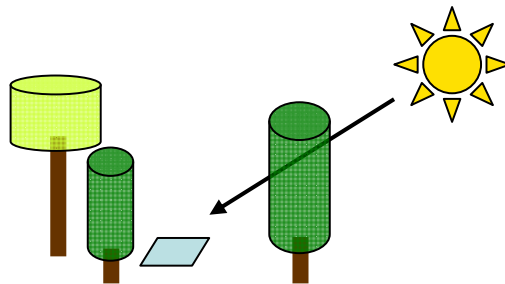
**Figure 21** GLI light submodel in SORTIE/NZ.
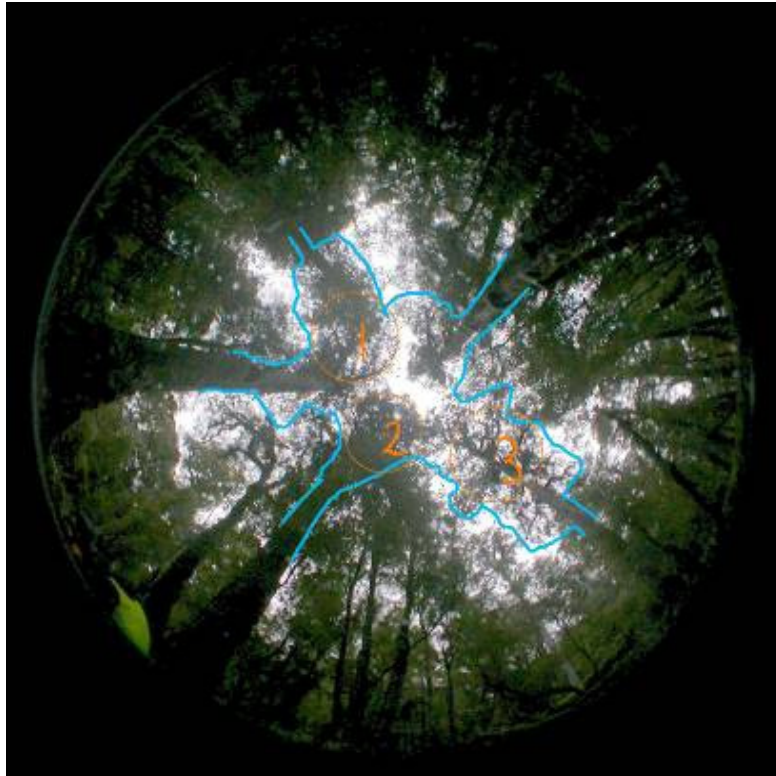
Figure 22 Example of fish-eye-lens photograph used for estimation of light transmission parameters.

Table 24 Light transmission coefficients estimated with fish-eye-lens photographs

	Mean % canopy openness	Standard deviation	Number of individuals
DACCUP	10.84	5.45	25
METUMB	8.43	4.56	15
NOTCLI	6.72	3.35	27
NOTMEN	7.6	3.87	65
PODHAL	8.22	4.5	27
PRUFER	6.24	4.9	9
WEIRAC	10.92	8.19	10

8.2 SORTIE/NZ GLI predictions

We used SORTIE/NZ to predict the light in three mapped plots in terrace forest using the actual spatial distribution of the trees and the crown allometry presented in the allometry section. We then compared the light distribution predicted by SORTIE/NZ with that measured using a quantum sensor in three mapped plots along the seedling measurement transects (Figure 23). Note that to test SORTIE/NZ light predictions, hemispherical photos are required rather than quantum sensor measurements.
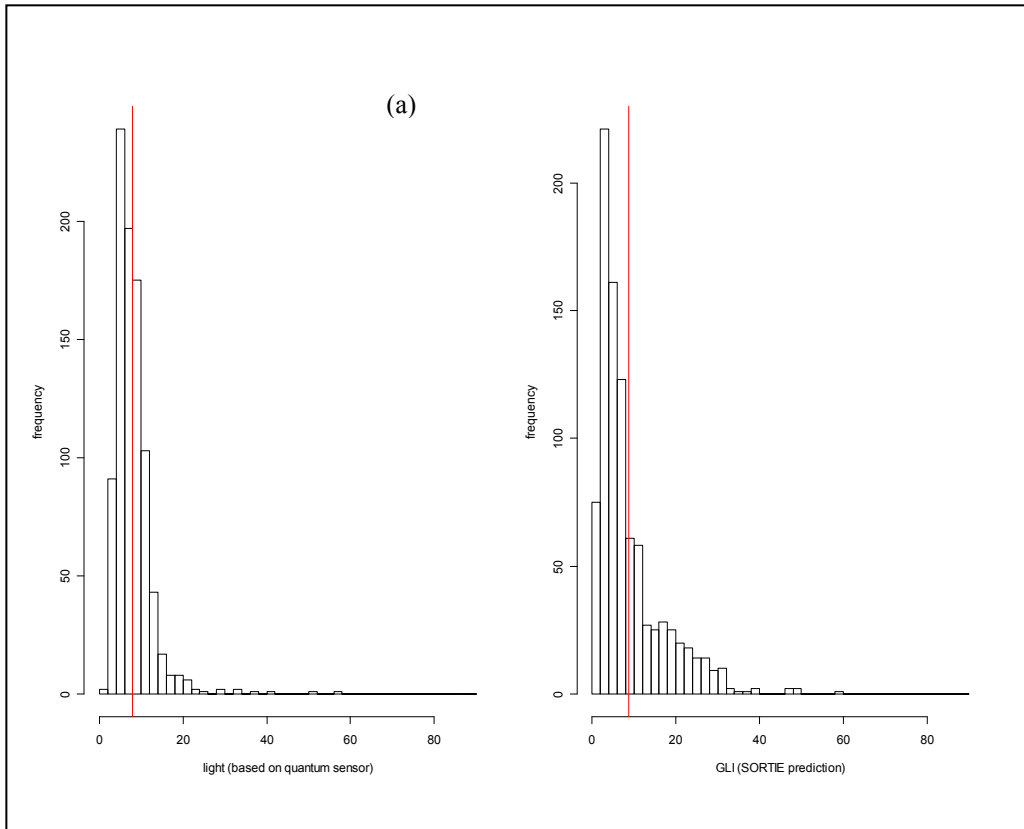
Figure 23 Observed and simulated distribution of percentage of light in three mapped plots of the terrace sites at Waitutu Forest, Southland. The observed light data are on the seedling measurement transects and were made using a quantum sensor.

9   Starting parameters

For each simulation, SORTIE/NZ requires that the starting conditions are defined. The model has a high sensitivity to the initial starting conditions, which can have important consequences for model projections.

9.1   Seedling initial population

For seedlings we used the same initial density for all species, because density was extremely variable within and between the three mapped plots (Table 25).

**Table 25** Seedling initial density per hectare in height classes used in SORTIE/NZ

Height class	Initial seedling density (no./ha)
16–45 cm	400
46–75 cm	400
76–135 cm	200

9.2   Sapling initial population

Based on the data of Coomes et al. (2005) (in small, 20×20 m, permanent plots), we computed the mean density per hectare for saplings in four size classes: 0–3, 3–5, 5–7.5 and 7.5–10 cm DBH. In order to include the large variability in sapling density observed in the field, an exponential distribution was fitted to the data (using function fitdistr in package MASS, Venables and Ripley 2002). Thus for each simulation we can draw initial sapling density (for each size class) from this exponential distribution (Table 26, Figure 24).

Table 26 Initial sapling density per hectare at Waitutu Forest and fitted parameters of the exponential distribution in SORTIE/NZ

	DACCUP	NOTCLI	NOTMEN	PODHAL	PRUFER	WEIRAC	METUMB
DBH size (cm)	Mean density/ha						
0–3	61	110	78	224	11	124	10
3–5	7.5	15	50	36.25	11.25	217.5	8.75
5–7.5	11.25	11.25	23.75	27.5	16.25	197.5	1.25
7.5–10	1.25	8.75	16.25	20	6.25	131.25	2.5
	Parameters of the exponential distribution						
0–3	0.0163	0.1000	0.0091	0.0129	0.0045	0.0889	0.0081
3–5	0.1333	0.1143	0.0667	0.0200	0.0276	0.0889	0.0046
5–7.5	0.0889	0.8000	0.0889	0.0421	0.0364	0.0615	0.0051
7.5–10	0.8000	0.4000	0.1143	0.0615	0.0500	0.1600	0.0076
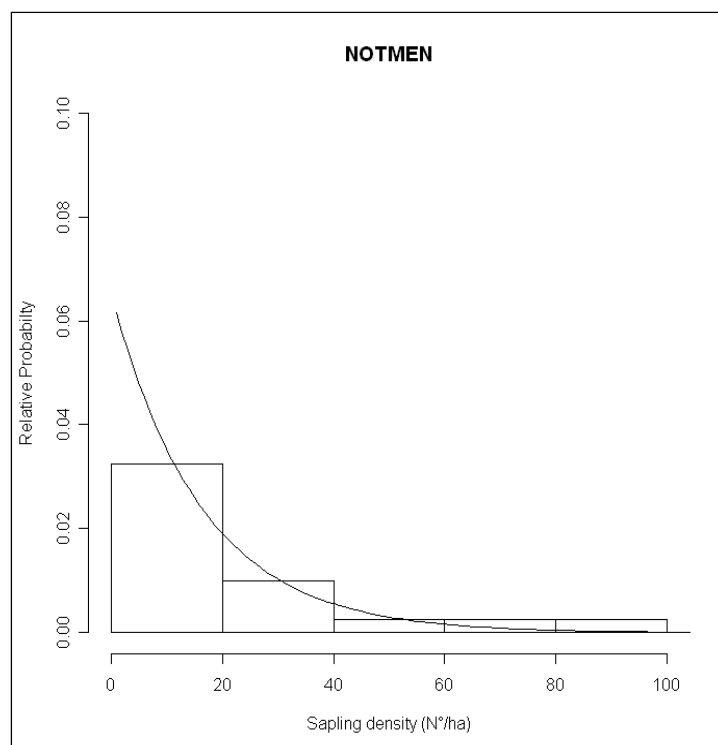
Figure 24 Example of observed distribution of sapling density (for the DBH size-class 7.5–10 cm) and fitted exponential distribution in SORTIE/NZ.

9.3 Adult trees

For adult trees we generated a 300 × 300 m simulated stand (Fig. 25) with characteristics similar to the three mapped stands. For each species the mean tree density is sampled within a normal distribution with a mean and a variance estimated from the three mapped plots, the spatial aggregation of trees of each species is based on the spatial aggregation of trees in the three plots (with one main radius of aggregation), and the DBH distribution is based on the observed distribution over the three plots. The spatial distribution of trees was generated with a Neyman–Scott cluster process in order to have a number of clusters and a radius of maximum aggregation similar to the spatial structure of the trees in the mapped plots. Note that one limitation of this method is that the interspecies spatial aggregation is not included.

9.4 Substrate

The initial conditions for substrate frequency are based on the data used in the seedling recruitment analysis, as the mean percentage of cover for each substrate in the terrace sites:

Initial conditions – Proportion of decayed logs = 0.14

Initial conditions – Proportion of fresh logs = 0.1

Initial conditions – Proportion of tip-up mounds = 0.06
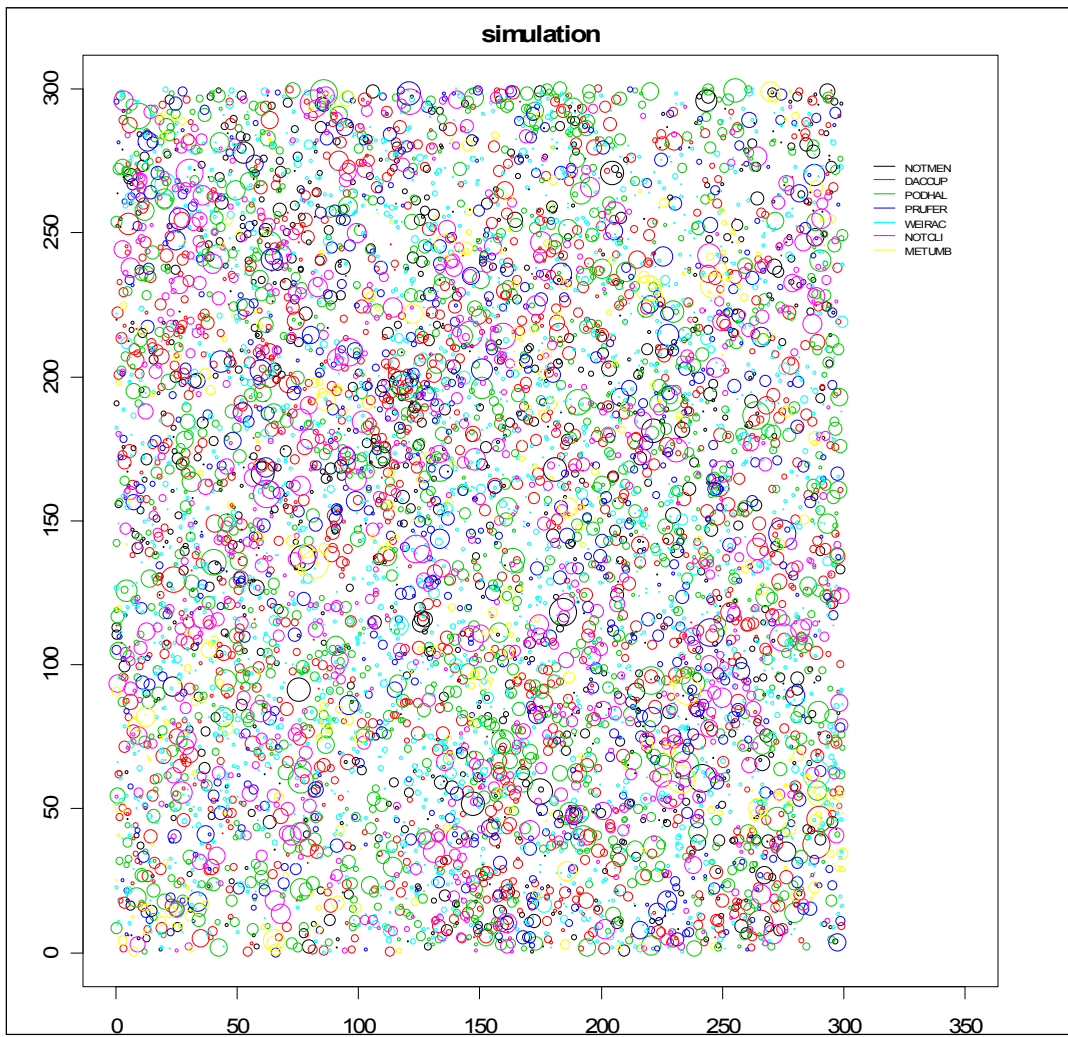
Maximum number of years for decay to occur = 300

Figure 25 Example of a map simulated with R code.
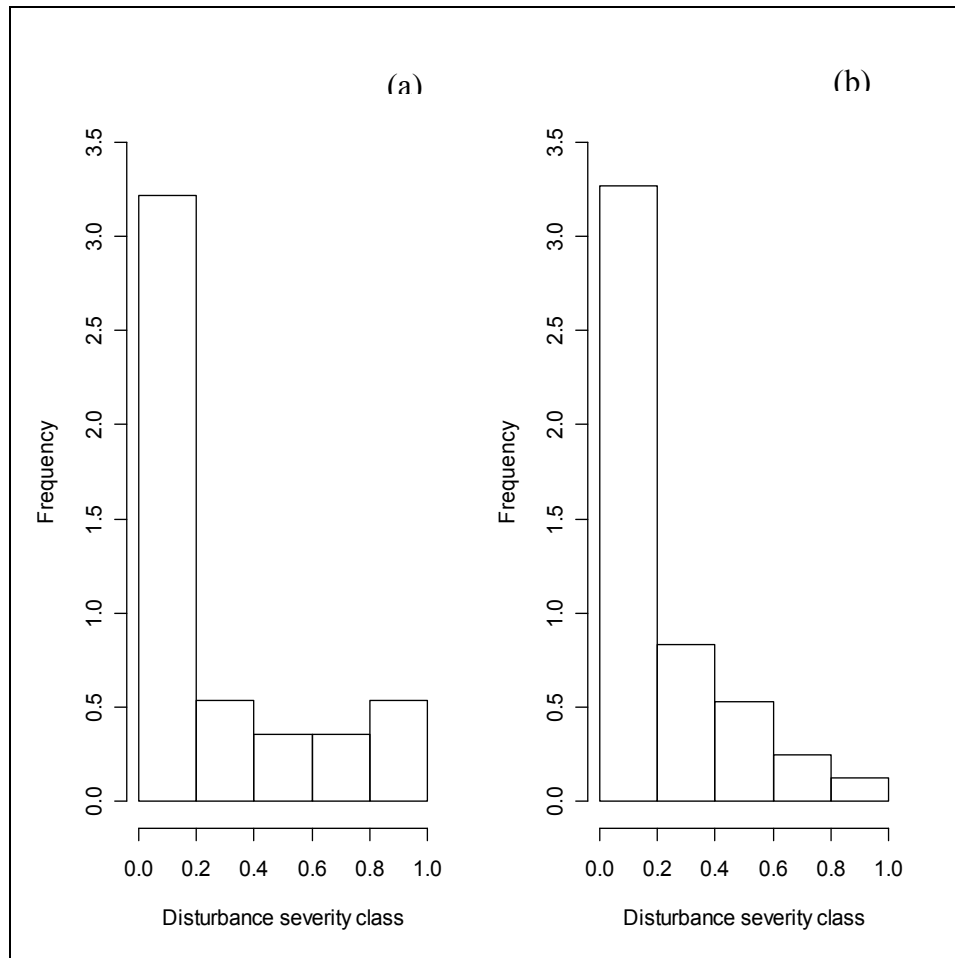
10   Disturbance

In SORTIE/NZ the disturbance behaviours are based on periodic disturbance by earthquakes, which are important in New Zealand forests. The only quantitative data available to estimate the effect are from the Basin Creek earthquake (Magnitude 6.7), but for only one species, NOTCLI (see Allen et al. 1999). We developed earthquake disturbance behaviours based on these data and applied estimates for NOTCLI to the other species given that no data were available to estimate species-specific response to earthquake disturbance. First a behaviour simulates the earthquake disturbance regime with a given return interval and spatial variation of the disturbance severity within the stand. Then behaviours simulate tree mortality as a function of earthquake severity, with different susceptibility of mortality between adults and juveniles (seedlings plus saplings).

10.1 Earthquake disturbance regime

Disturbance return interval.—The parameterisation of this disturbance regime is based on the return interval for earthquakes given by Stirling et al. (2002) for the Waitutu Forest. The main seismic faults have a return interval of 500 years for earthquakes greater than Magnitude 7.0. Thus we decided to use a return interval of 500 years. In order to simulate an earthquake that applies to a large area when we run replicated simulations of the earthquake, we applied exactly the same time-step to all the simulations. Thus assuming that each replicate run represents a sample of a large landscape subject to large-scale earthquake disturbance. We randomly selected the times of earthquake occurrence based on a 500-year interval and then applied these occurrence times to all the simulations (for a 600-years' simulation we applied disturbance at year 405).

Spatial variability of the disturbance severity.—The spatial variability of disturbance severity was simulated by using a disturbance severity index (on a scale of 0 = no damage to 1 = total damage) to represent variation in the local severity of the effect of the disturbance. This is based on data from plot remeasurements (permanent plots, 20 × 20 m) quantifying the immediate effects of the Arthur's Pass earthquake on Basin Creek forests (Allen et al. 1999). The severity of the disturbance was quantified for each 20 × 20 m plot based on the percentage of stem biomass mortality (Disturbance Severity Index). Frequency declined with Disturbance Severity Index (Figure 26a). The spatial variability in disturbance severity between the 20 × 20 m cells in the 300 × 300 m stand was simulated in SORTIE/NZ by randomly drawing the Disturbance Severity Index from a truncated normal distribution fitted to the observed frequency distribution. The mean of the normal distribution was randomly chosen between 0 and 0.1 and its variance was estimated to fit the frequency of the 28 Basin Creek plots (20 × 20 m) (Figure 26b).
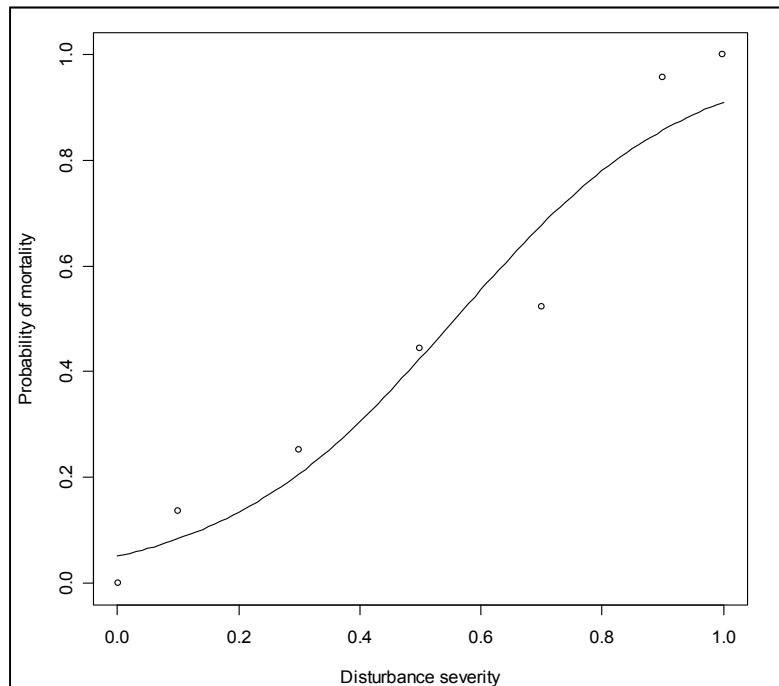
Figure 26 Frequency of disturbance severity for the disturbed plots observed in Basin Creek (a) and simulated with a truncated normal function (b). The index of disturbance severity is based on percentage of stem biomass mortality from Allen et al. (1999). The SD of the normal distribution is 0.3783 (and its mean is randomly chosen between 0 and 0.1). The simulation corresponds to the average (over 1000 repetitions of the disturbance) frequency distribution of the severity class over 1000 20 × 20 m cells.

10.2 Earthquake adult-tree mortality

This behaviour decides which trees are killed when an earthquake has occurred. According to Allen et al. (1999) there is no DBH effect on the probability of mortality with earthquake disturbance for the Basin Creek data. The mean percentage tree survival for 10 disturbance severity classes (based on percentage of stem biomass mortality) was used to estimate the parameters of a function relating adult tree probability of survival to the Disturbance Severity Index. The probability-of-survival ($p(d)$) function is:

$$p(d) = \frac{\exp(a + b * c)}{1 + \exp(a + b * c)},$$

where *a* and *b* are estimated parameters and *c* is the Disturbance Severity Index. The parameters were estimated for NOTCLI (Figure 27, Table 27), but the same values were used for all the species. For the analysis, the observations are weighted by the number of plots used to compute the mean survival of each class

Figure 27 Probability of mortality as a function of disturbance severity for NOTCLI based on Basin Creek data (Probability of mortality = 1 – Probability of survival).

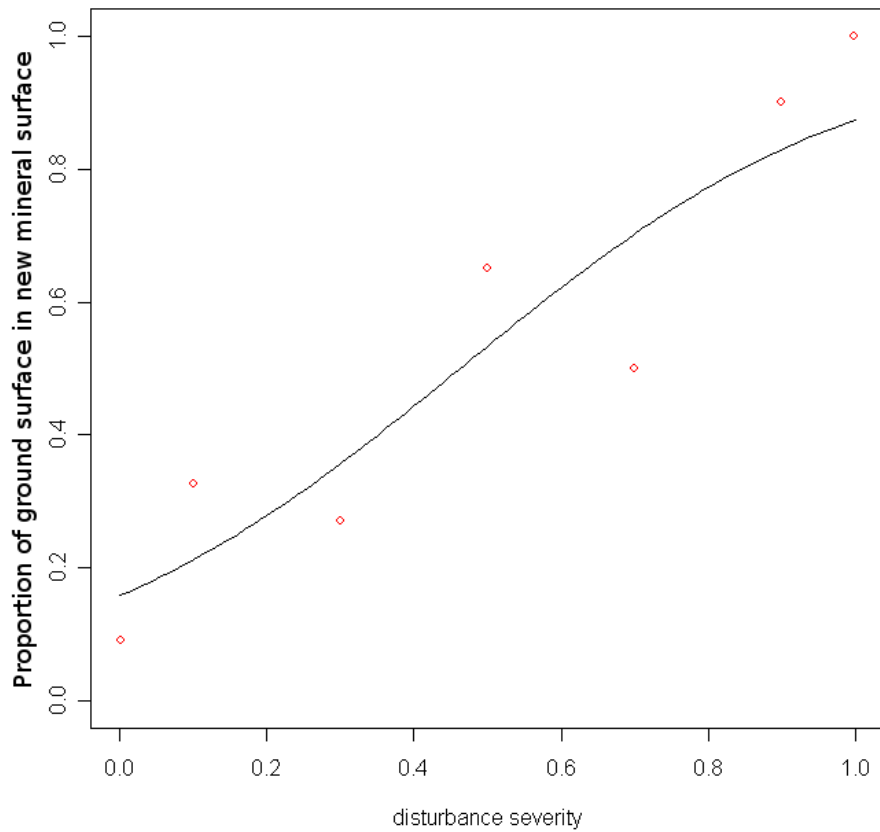**Table 27** Disturbance parameters estimated

	a	*b*
NOTCLI	2.903	−5.209

10.3 Earthquake juvenile mortality

The proportion of ground surface in new mineral surfaces in the plots after the earthquake was used as a surrogate for probability of juvenile (seedling and sapling) mortality. This proportion of ground surface (*p*) was related to severity of disturbance on the plot, using the following function:

$$p = \frac{\exp(a + b * c)}{1 + \exp(a + b * c)},$$

where *a* and *b* are estimated parameters and *c* is the Disturbance Severity Index. Parameters were estimated with maximum likelihood methods and were used to represent juvenile mortality after earthquake disturbance.

Figure 28 Proportion of ground surface in new mineral surfaces as a function of disturbance severity based on Basin Creek data for NOTCLI. The proportions of ground surface in new mineral surfaces in the plots after the earthquake were used as a surrogate for probability of juvenile mortality.

The estimated parameters are:

$a = -1.721$

$b = 3.705$

11 Harvesting

The podocarp harvesting scenarios were based on the Sustainable Forest Management prescriptions implementing the 1993 Amendment to the New Zealand's Forests Act 1949. A short description of the prescriptions follows.

11.1 Prescriptions for sustainable forest management

Prescriptions for sustainable forest management are implemented through standards and guidelines (Ministry of Agriculture and Forestry 2002). These guidelines generally dictate that podocarps shall be harvested:

- As individuals or small groups of up to 5 trees

- Across the diameter range of trees >30 cm in diameter

- Retaining a proportion of the largest (senescent) trees as wildlife habitat

- As a periodic harvest: 5% of live standing basal area (>30 cm in diameter) may be harvested (harvesting intensity) every 10 years (return cycle) giving a harvest rate of 0.5% per year

11.2 Simulations of sustainable forest management

Based on these prescriptions we applied the following harvesting scenario in SORTIE/NZ for podocarps (DACCUP, PODHAL, and PRUFER).

We applied harvesting on the whole 300 × 300 m simulation stand in each 10 years. The harvesting removes 5% of the basal area of the trees with DBH > 30 cm and < 90 cm, and only 2.5% for the trees with a DBH > 90 cm, in order to retain a proportion of the largest (senescent) trees as wildlife habitat.

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