Consequences of deer control for Kaweka mountain beech forest dynamics

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ABSTRACT

We used measurements on permanently tagged mountain beech seedlings from 99 plots in Kaweka Forest Park (monitored between 1997 and 2004) to model seedling growth, recruitment and survival under three deer control treatments (fenced plots from which deer were excluded, aerial hunting and recreational hunting). In 2005/06 mountain beech forests in Kaweka Forest Park were surveyed using 189 systematically located plots. Twenty of these plots (10.6%) had low basal area (<44 m^2) and insufficient seedlings above deer browse height (1.35 m) to ensure canopy replacement. The seedling growth, recruitment and mortality models were applied to each of these 20 plots to estimate how many years it would take for a sufficient number of seedlings to grow above deer browse height to ensure canopy replacement under each of the three deer-control treatments. Fencing resulted in the fastest recovery followed by aerial then recreational hunting. The consequences of varying the recovery time were explored using a whole-forest simulation model in which canopy openings were formed by natural disturbance, which then recovered (i.e. gained sufficient seedlings above deer browse height to ensure canopy replacement) at a rate determined by the deer control treatment. One consequence of delaying recovery times by using less intensive deer control is to increase the amount of forest in an open state (i.e. low basal area) at any one point in time. We discuss other likely consequences of delaying the recovery times.

Keywords: deer control, mountain beech, regeneration, herbivory, forest dynamics, Kaweka Forest Park

1. Introduction

Landcare Research was contracted by the Department of Conservation to (1) design a sampling programme to estimate the percentage of mountain beech area of Kaweka Forest Park that does not have sufficient mountain beech seedlings to establish a replacement canopy, (2) develop protocols to implement the sampling programme, and (3) design a template for data entry. This work was completed in November 2005. In this report we provide an analysis of the mountain beech data to guide managers on future deer control. We assess the ecological gains from the recruitment rates possible from three levels of deer control, and report on the consequences of a time delay in adequate regeneration. This work was completed between July 2005 and June 2006.

1.1 ANALYSIS OF THE MOUNTAIN BEECH DATA

We present the analysis in several parts. First, for completeness we summarise the mountain beech seedling growth, recruitment and mortality models that we developed using data from the Kaweka Mountain Beech Project that were presented to the Department of Conservation in a report in 2005 (‘Summary of Kaweka mountain beech analysis’). We then present a summary of the 2005/06 data followed by a description of the application of the seedling models to the 2005/06 data. We then assess the ecological gains from different levels of deer control and report on the consequences of a delay in the time taken for a sufficient number of seedlings to grow above deer-browse height to achieve adequate canopy replacement. Finally, we report on an analysis of the response of noncanopy species to deer control.

2. Summary of the growth, recruitment and mortality models

2.1 GENERAL APPROACH TO GENERATING MODEL PARAMETERS FROM THE KAWEKA MOUNTAIN BEECH PROJECT

Ninety-nine vegetation plots (20 × 20 m) were subjectively located by Department of Conservation staff on a range of sites in the open-canopied mountain beech forests of Kaweka Forest Park during the summers of 1996/97 and 1997/98. When established, these plots were used to measure the initial forest structure in terms of the number of seedlings (as well as their height) and the basal area of trees (based on diameter measurements). Whether (and when) a plot has an adequate number of stems above deer-browse height to replenish the canopy was determined by the recruitment, growth and mortality of all browse tier seedlings, as well as how many stems were required for canopy replacement on a plot. So we determined:

- Annual recruitment, growth and mortality of tagged seedlings for projecting the number and size of seedlings into future years;
- The minimum number of stems required above deer browse height (1.35 m) on each plot from the initial basal area of trees. We set deer browse height at 1.35 m for two reasons. First, in the 2005/06 survey this was the height to which seedlings were measured and this height therefore defines the threshold between seedlings and taller stems for these data. Second, the choice of 1.35 m is justified by observations suggesting that deer rarely browse higher than this, and our data showing that seedling growth increment levels off around this height (see below).

The end point is a model that combines the initial number and height of seedlings in a plot with the modelled rates of seedling recruitment, growth and mortality, as well as initial basal area, to produce an estimate of the time taken for a plot to achieve the minimum number of stems required above browse height to replace the canopy. We apply this model to the sample plot data collected in the summer of 2005/06 and compare the time taken for plots to achieve canopy replacement under three different deer-control treatments: inside fenced exclosures, aerial hunting, and non-treatment areas with recreational hunting only.

2.2 ANNUAL RECRUITMENT, GROWTH AND MORTALITY OF TAGGED SEEDLINGS

We statistically tested whether relationships between seedling height and recruitment, growth and mortality varied among the three deer-control treatments, among years, with basal area, or with site factors (altitude and potential solar radiation).

Deer-control treatments considered in the analysis were:

1. ‘Fenced’ plots
2. ‘Aerial hunted’ areas
3. ‘Recreational hunted’ areas (which includes all plots in the original Enhanced Recreational and Commercial recovery areas, and recreational hunting areas).

2.3 RECRUITMENT

In Figure 1, we show the percentage of plots that received different numbers of seedling recruits in each year. Recruitment was modelled using non-linear maximum likelihood estimation assuming a negative binomial error structure. Recruitment rates varied significantly among years, but did not vary with deer control treatment, basal area or site conditions. We present these relationships for all 99 plots in each of the three years for which we have data (recruitment data were not collected in 2003/04). In each year, most plots had few recruits (<10 seedlings), although in 1999/2000 a much greater percentage of plots recruited >10 seedlings, probably reflecting the heavy seeding year in 1997/98.

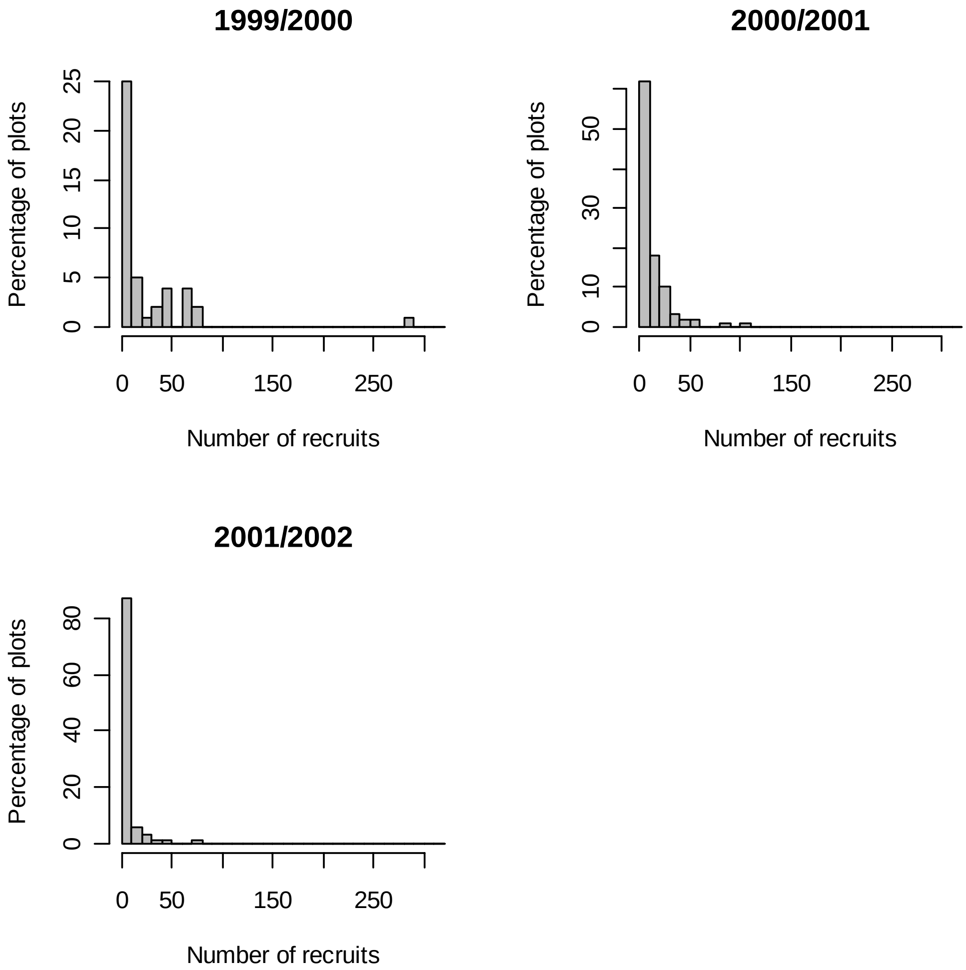

Figure 1. Percentage of 99 plots that received different numbers of seedling recruits in each of three years.

2.4 GROWTH

Annual height increment (growth) was modelled using a non-linear four-parameter model; the Gompertz Function, fitted by non-linear maximum likelihood estimation. Annual growth was strongly correlated with seedling height (Fig. 2), with the form of this relationship varying significantly among the three deer-control treatments, and with plot basal area and year. Figure 2 shows the raw data (solid dots) and the fitted relationships (lines) between height increment and seedling height for the three treatments for plots of low (20 m^2/ha; solid line), intermediate (40 m^2/ha; long dash) and high (60 m^2/ha; small dash) basal area. In all treatments, seedlings grew faster in lower basal area plots. The form of the growth curves varied slightly among years, but we only show the curves for the 2000/01 year.

Height increment is low for small seedlings, increases and then levels off at about 10 cm/year (Fig. 2). The main difference among treatments is that small seedlings (<50 cm tall) have slower growth in the aerial and recreational hunted areas respectively, relative to the fenced area, and the height at which growth increment begins to accelerate occurs at greater seedling height in these treatments.

In summary, the presence of deer in the recreational-hunted and aerial-hunted treatment areas retarded seedling growth in smaller seedlings (<50 cm) compared with seedlings completely protected from deer (fenced plots).

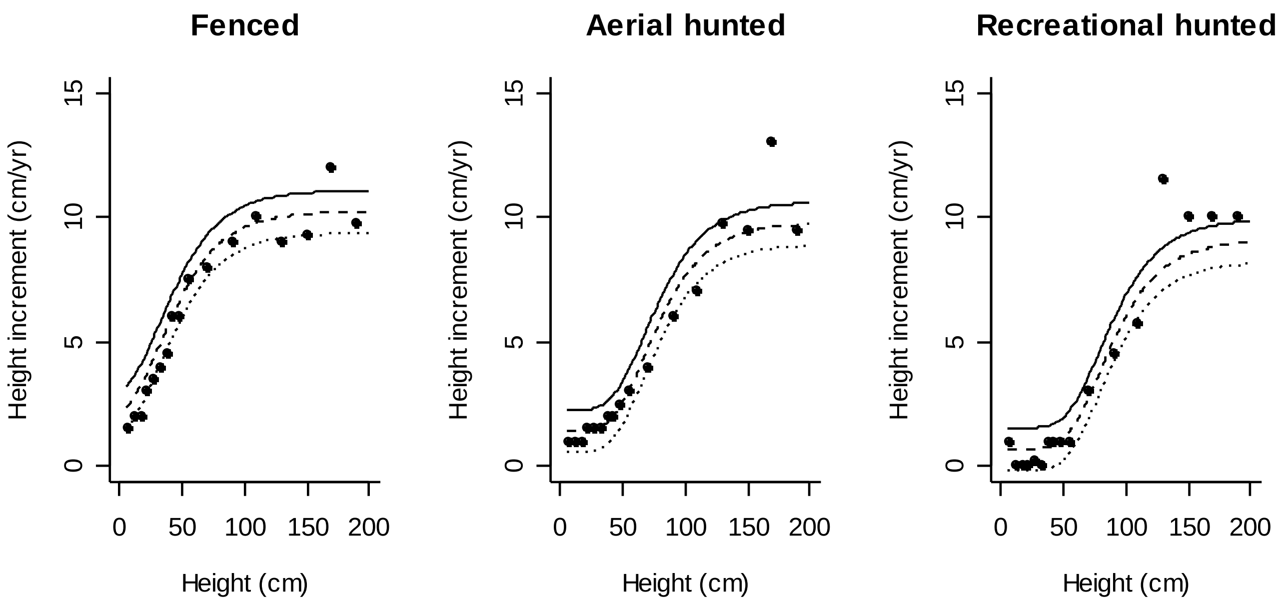

Figure 2. Relationship between annual height increment and seedling height for mountain beech seedlings under three deer-control treatments. Solid dots show mean height increment derived from the raw data, lines show the fitted relationships for plots of low (20 m^2/ha; solid line), intermediate (40 m^2/ha; long dash) and high (60 m^2/ha; small dash) basal area.

2.5 MORTALITY

There was a strong relationship between seedling height and annual rate of seedling mortality (Fig. 3) with small seedlings having the highest rates of mortality. Having accounted for variation in seedling height, mortality also varied among years but not among deer control treatments, or with basal area or site conditions (mortality was modelled using a generalised linear model with a binomial error distribution). We therefore present the rate of mortality, calculated using all 99 plots, shown as a function of seedling height for each of the three years for which we had suitable data (Fig. 3). In all years, mortality rates were high (>5% mortality) in very small seedlings but levelled out to a very low rate (<1% mortality) for seedlings >50 cm height.

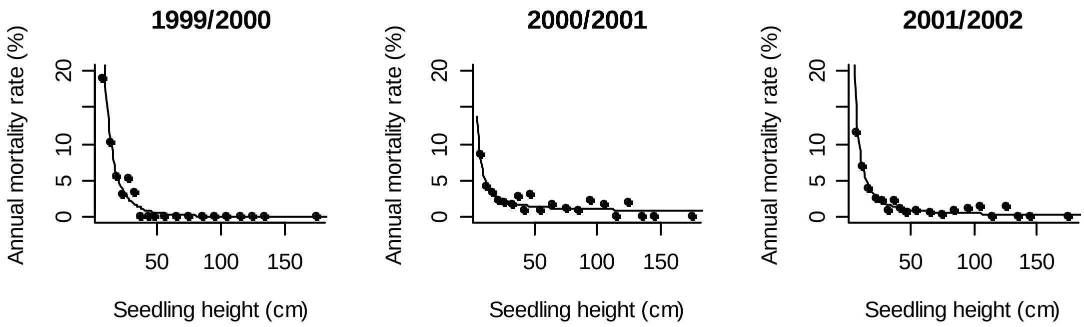

Figure 3. Annual rates of seedling mortality in relation to seedling height for mountain beech seedlings in three census years.

2.6 DIRECT AND INDIRECT EFFECTS OF DEER

Deer had a direct effect on seedling performance by slowing seedling height growth. While deer did not have a direct effect on seedling mortality (there was no difference in mortality rate among deer-control treatments having accounted for variation in seedling height), deer nevertheless had a strong indirect effect. This occurred because deer slowed seedling height growth in the aerial and recreational hunted areas, keeping seedlings smaller for longer. Because smaller seedlings suffered higher rates of mortality (Fig. 3), overall seedling mortality was highest under recreational hunting, intermediate under aerial hunting and lowest under fencing.

2.7 MINIMUM NUMBER OF STEMS REQUIRED ABOVE DEER BROWSE HEIGHT

The number of stems above browse height (1.35 m) required for canopy replacement on each plot depends on the number of existing saplings and canopy trees. A fully stocked mountain beech stand was defined as having a minimum basal area of 44 m^2/ha based on the data in Wardle (1984). This value is slightly less than the mean basal area for pure mountain beech stands that Wardle (1984) presents (47.6 m^2/ha; page 308), but we used this lower value because stands could be readily identified as having a basal area greater or less than 44 m^2/ha using a basal area prism in field sampling (see below). Fully stocked mountain beech stands in Kaweka Forest Park have a mean stem density of 20 stems/100 m^2 (calculated from 23 permanent plots located in mountain beech forest in Kaweka Forest Park with a basal area ≥44 m^2/ha that were measured in 1981). In this case, 20 stems represents the **minimum** number of trees that need to be recruited into the canopy where there are no existing trees on a plot and assuming that none of these stems die during subsequent stand development. If a plot already has a fully stocked basal area (≥44 m^2/ha) we assume it does not require any further stems to recruit. The number of stems above browse height required in any plot can therefore be determined from a simple relationship that assumes a linear relationship between basal area and stem density (Fig. 4). This relationship (Fig. 4) was used to set the target number of 1.35-m-high seedlings required for each plot in the simulation models below.

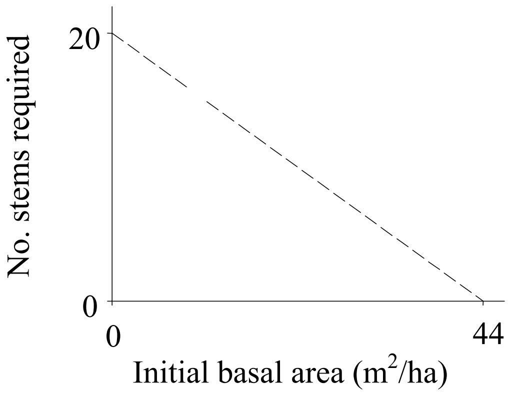

Figure 4. Relationship between initial basal area of a plot and the number of stems required for that plot to achieve a basal area of 44 m^2/ha, i.e. a fully stocked basal area.

3. Summary of the 2005/06 data

The growth, recruitment and mortality models above were derived from data collected in 99 plots that were subjectively located to sample relatively open mountain beech forest in Kaweka Forest Park. As such, these plots do not provide a representative sample of mountain beech forest in the Kawekas – they tend to sample more open areas. In order to determine the likely consequences of different deer-control treatments in Kaweka Forest Park we need a representative sample of plots from mountain beech forest so we can estimate (1) what proportion of mountain beech forest in Kaweka Forest Park is currently in an 'open' state (i.e. with a basal area <44 m^2/ha) and requires additional stems to grow above deer browse height to ensure canopy replacement and (2) how long it will take for these 'open' plots to recover (i.e. to get a sufficient number of stems above deer browse height to achieve canopy replacement = basal area ≥ 44 m^2/ha) under the three different deer-control treatments?

In the summer of 2005/06, staff of the Department of Conservation visited 230 sites located systematically throughout Kaweka Forest Park in areas mapped as mountain beech forest in order to obtain a representative sample of the mountain beech vegetation. At each site tree basal area was recorded using a basal area prism. One hundred and eighty nine of the sites were in mountain beech forest (Table 1) of which 30 (16%) had a basal area <44 m^2/ha (Figs. 5 and 6).

Table 1. Summary of vegetation types found in 230 systematically located sites sampled in 2005/06

Category	No. plots	% plots
Red beech	22	9.5
Inaccessible	19	8.5
Mountain beech	189	82.0
Total	230	100.0

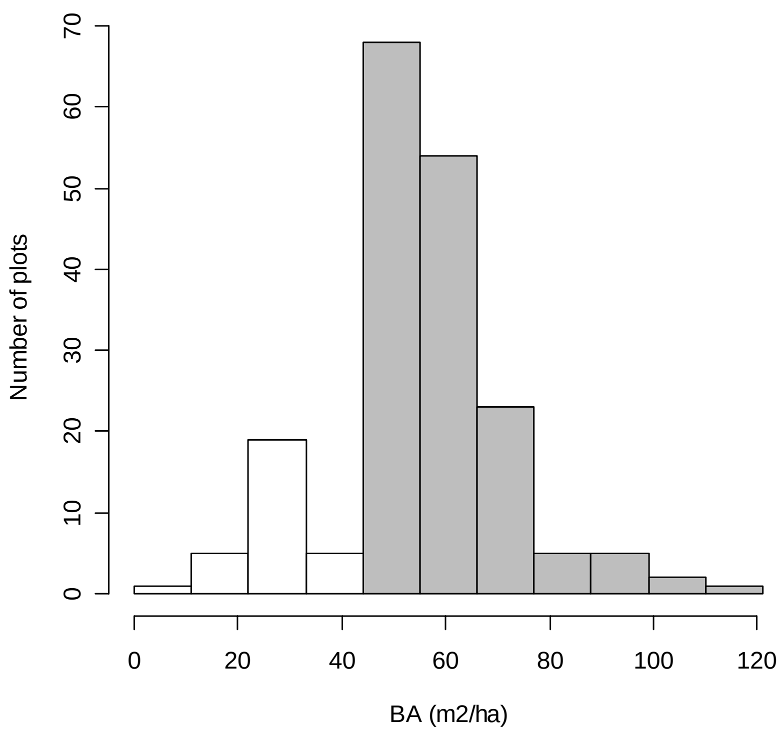

Figure 5. Frequency distribution of the basal area (BA) of the 189 mountain beech plots. BA <44 m^2/ha shown as open bars; BA ≥44 m^2/ha shaded.

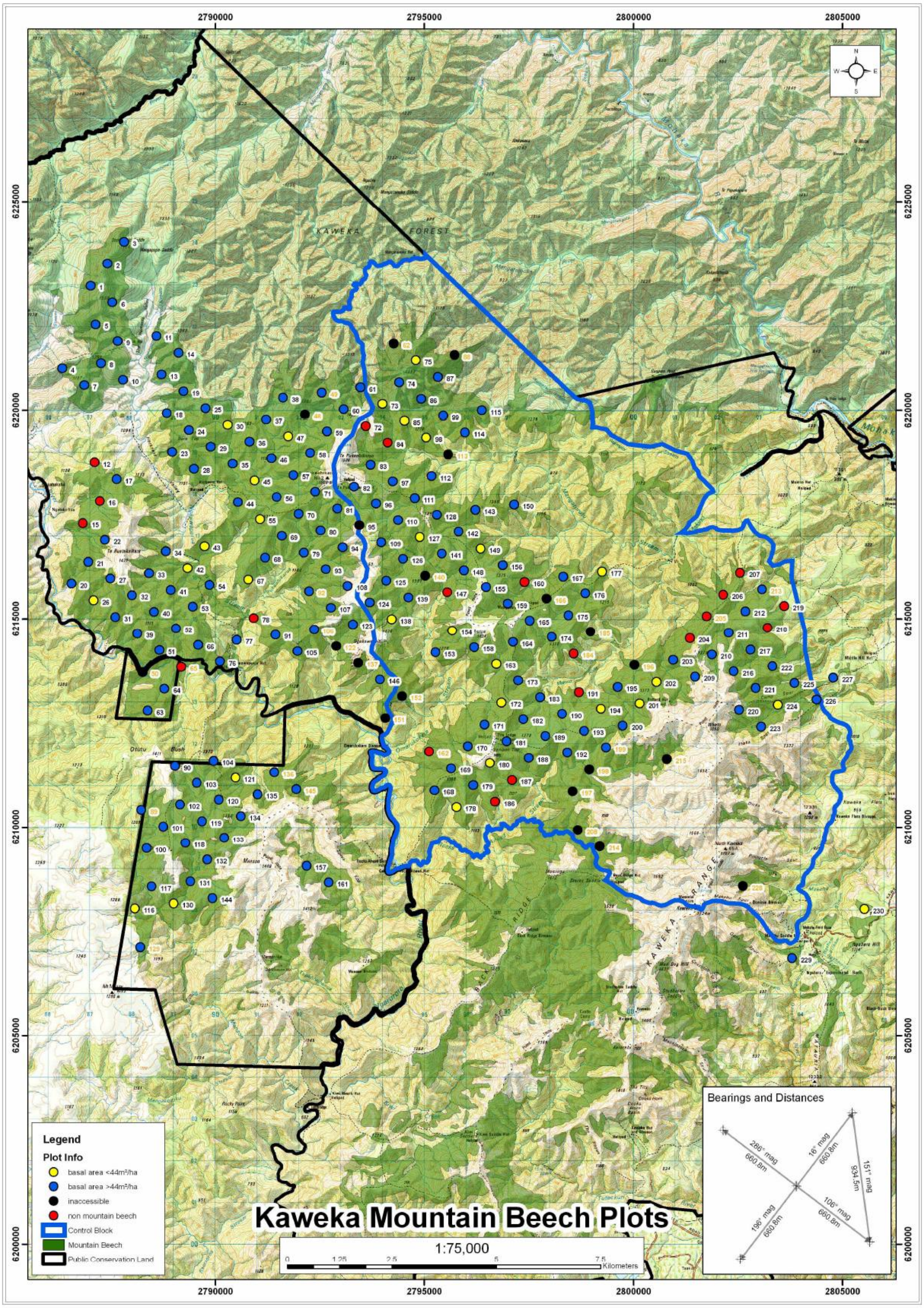

Figure 6. Location of sites sampled in the 2006/06 survey and their classification by basal area.

On those mountain beech plots with a basal area <44 m^2/ha, mountain beech seedlings (≤1.35 m) in a 10 x 10 m plot were counted and their heights recorded. On plots with very large numbers of seedlings, a subsample of the plot was measured.

Of the 30 mountain beech plots with basal area <44 m^2/ha, nine already had sufficient stems >1.35 m in height to ensure canopy replacement and one plot did not have seedlings measured and was therefore excluded from further analysis. This left 20 plots (10.6%) that required some seedlings to grow to 1.35 m to ensure there were sufficient stems above deer browse height for canopy replacement. We modelled the number of years it would take each of these 20 plots to reach the threshold number of stems required for canopy replacement under each of the three deer control treatments.

3.1 APPLYING THE MODEL TO THE 2005/06 DATA

We used the following information to model future seedling dynamics on these 20 plots:

- Initial number of seedlings and their individual heights on each plot
- Growth and mortality functions derived from the Kaweka Mountain Beech Project (Section 2) were used to model the annual growth and survival of individual seedlings on each of the 20 plots, and new individuals were recruited each year into plots according to the recruitment function. These functions take into account variation in growth, mortality and recruitment related to deer-control treatment, year of measurement, basal area, and random site (plot) effects.

Plots were ‘grown’ into the future for 100 years. On each plot we calculated how many years it took to achieve the minimum number of seedlings above browse height (1.35 m) required for canopy replacement. Note that under some treatments, some plots failed to reach the minimum number of seedlings after 100 years. For these plots, 100 years is the minimum recovery time.

The result of the model is a frequency distribution of the years taken for plots to achieve the minimum number of seedlings above browse height required for canopy replacement.

We modelled the 20 plots applying each treatment in turn: fenced, aerial hunted and recreational hunted. That is, starting at our baseline year of 2006, we ‘grew’ the plots assuming that all plots were fenced, that all plots were aerial hunted, and that all plots were recreational hunted, and compared the outcomes.

3.2 ASSESSMENT OF THE ECOLOGICAL GAINS FROM THREE LEVELS OF DEER CONTROL

In the following section, we investigate the effect of applying each treatment in turn to all 20 plots. We assume that in the absence of any specific deer management in Kaweka Forest Park, recreational hunting will occur at present intensities. We therefore compare the effects of (1) fencing all plots, and (2) aerial hunting all plots, relative to the effects of (3) only recreational hunting on all plots.

3.2.1 How long does each plot take to recover under the three treatments?

Figure 7 shows how long it would take for each of the 20 plots to obtain an adequate number of stems >1.35 m in height under recreational hunting, aerial hunting, and fencing. With fencing, all plots obtain an adequate number of stems within 40 years, and most (18/20) within 20 years. With aerial hunting 18/20 plots obtain an adequate number of stems within 40 years with most taking between 20 and 40 years, while with recreational hunting most plots (13/20) take longer than 40 years, with four plots taking longer than 80 years.

Figure 7. Frequency histograms of the time taken for each of the 20 plots to obtain an adequate number of stems >1.35 m in height under recreational hunting, aerial hunting, and fencing. Note that under recreational hunting, some plots failed to reach the minimum number of seedlings after 100 years. For these plots, 100 years is the minimum recovery time.

3.2.2 What determines recovery time?

It is important to consider the features of a plot that influence the time taken to achieve an adequate number of stems. We examined whether the initial number of seedlings on a plot and plot basal area were predictors of the time taken by a plot to recover under the different treatments. We expect these variables to be important because plots with more seedlings have a larger pool of potential recruits, and because plots with initially higher basal area require fewer additional stems to ensure canopy replacement.

By far the strongest and most significant predictor was the initial number of seedlings per plot; plots with few seedlings take longer to recover (Fig. 8) and this effect is greatest under recreational hunting.

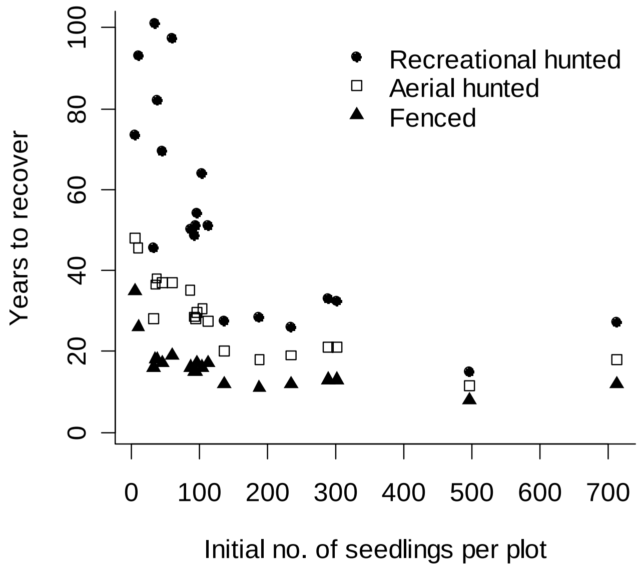

Figure 8. Relationship between initial seedling abundance on a plot and the time taken for that plot to recover under three levels of deer-control.

3.2.3 Comparing gains from aerial hunting and fencing

Those plots that take the longest time to recover under recreational hunting benefit the most from either aerial hunting or fencing, although fencing produces greater gains (up to 80 years faster recovery relative to recreational hunting; Fig. 9).

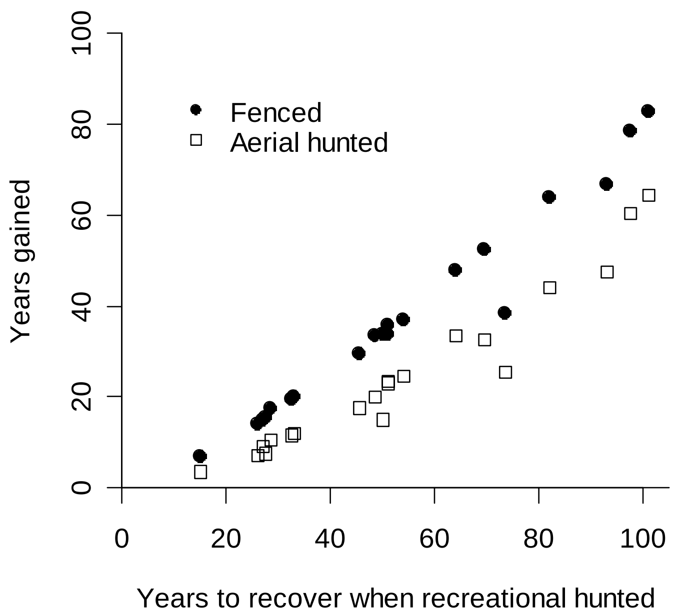

Figure 9. Number of years gained by fencing and by aerial hunting relative to the baseline of recreational hunting. For each plot, our definition of gain is the difference in years between treatments to achieve an adequate number of stems for canopy replacement.

4. What are the consequences of a time delay in achieving adequate regeneration?

The results show that:

- 10.6% of mountain beech forest is currently in an ‘open’ state, without sufficient stems above deer-browse height to ensure adequate canopy replacement.
- Deer effects on individual seedling performance are determined largely via growth rate rather than mortality or recruitment.
- Plots differ in the time taken to recover from this ‘open’ state, with the rate of recovery largely determined by the initial number of seedlings in a plot.
- Recovery time is also strongly affected by deer-control treatment. On any given plot, fencing would achieve the fastest recovery, followed by aerial hunting, then recreational hunting.

Within the context of these results we now ask what are the consequences of delaying the recovery time, or equivalently, what are the consequences of shortening the recovery time by switching, for example, from a recreational to an aerial hunting regime? From an ecological perspective these consequences may manifest themselves at several levels: populations (numbers of individuals and their dynamics), communities (species composition) or ecosystems (includes the dynamics of abiotic components), all of which interact. In considering the consequences at these levels we draw upon literature from Kaweka Forest Park mountain beech forests, mountain beech forests elsewhere, and information from forests more generally where we consider the information strongly relevant. Certainly it would be best if such information all came from Kaweka Forest Park – but this is simply not available.

4.1 MOUNTAIN BEECH POPULATION CONSEQUENCES

Results of the work so far reported here have largely characterised population-level consequences for seedlings and trees at the individual- and plot-scales using data specific to Kaweka Forest Park. Certainly the population-level consequences can also be considered at a patch scale and in terms of the total Kaweka Forest Park mountain beech forest. By patch we mean the particular landscape unit sampled by a plot that has vegetation structurally similar to the plot. Patches of ‘open’ forest often form an abrupt boundary with an intact forest of tall trees, creating a matrix of forest areas having different heights and structure. These boundaries can sometimes cause high mortality in the edge trees through, for example, periodic disturbance to the exposed edge trees through storm events and expansion of the patch (Wardle 1984). In such instances any delay in recovery time of the mountain beech forest increases the time interval that patch edge trees are exposed. Field observations suggest that the patches range in spatial scale from the plot area to >1 ha. We could expect that seed supply is limited in some large open patches with few seedlings because: (1) some patches only have a few residual trees; (2) it will take some time before seedlings grow to a size where they will produce seeds; and (3) 90% of beech seeds fall with 20 m of the parent tree (Wardle 1984).

Our predictions about the rate of recovery of low-basal-area forest within the Kaweka mountain beech forest have so far ignored the population dynamics of the forest matrix within which forest of low basal area is found. The current issues arose due to a perceived lack of adequate regeneration in canopy openings in mountain beech forest in Kaweka Forest Park resulting from apparent senescence in stands of large mountain beech trees that were attacked by defoliating moths (Hosking & Hutcheson 1988). While damage as severe as that in 1980s may or may not be unusual, ongoing natural events such as local windstorms and snowfalls will continue to cause mortality of mountain beech trees and to form canopy openings in the forest. Hence, at the same time as the present set of canopy openings are recovering back to closed canopy forest, other canopy openings will be forming in other parts of the forest as a result of these ongoing natural mortality processes. At any point in time, the total proportion of forest that is in an 'open' state represents a balance between the rate at which canopy openings are formed by natural processes and the rate at which they recover. An important consequence of changing the time that it takes for canopy openings to recover is that, over time, this will alter the proportion of forest that is in an 'open' state. If the length of time taken to recover increases, the amount of forest in an 'open' state will also increase.

It is not possible to predict precisely how much open forest will occur in Kaweka Forest Park in the future because, in addition to the rate of recovery, this depends critically on the timing and severity of disturbances that kill trees and form canopy openings, and these are unpredictable events. In the absence of disturbance the forest will close up as existing open areas recover, while the occurrence of a major windstorm or insect outbreak, for example, could initiate widespread tree mortality and cause extensive opening up of the forest.

Because the timing and severity of disturbances are unpredictable, the precise future trajectory of the forest cannot be determined. However, we can examine how the forest will respond to particular disturbance scenarios that we provide, and we can compare how that response will differ under different deer control treatments, providing a basis for assessing the likely consequences of a time delay in regeneration.

We illustrate this using a simulation model in which we consider a hypothetical area of Kaweka mountain beech forest comprising 1000 patches each the size of a 10 × 10-m plot. Each patch can be in one of two states: 'open' (with a basal area <44 m^2/ha) or 'closed' (with basal area ≥44 m^2/ha). Each year, some proportion of patches are disturbed by a natural event (such as a windstorm or snowfall). A disturbance kills trees and forms a canopy opening, converting a 'closed' patch into an 'open' patch. The 'open' patches then begin to recover, with the time taken to recover back to a 'closed' state determined by the number of years that we actually estimated plots would take to recover in our modeling (Fig. 7). Starting with the proportion of 'open' forest in 2006 (10.6% as determined in the 2005/06 survey), we can then run our simulation model into the future and examine how the proportion of forest in an 'open' state changes through time, representing the balance between the rate at which patches are disturbed and the rate at which they recover. We can do this separately for each of the deer-control treatments, by using the recovery times specific to each treatment, and thus examine how deer control (which alters recovery time) affects the amount of forest in an 'open' state under a particular disturbance scenario.

The simulation model requires that we provide a disturbance scenario by specifying how much of the forest is disturbed each year. Forests are naturally subject to a range of disturbances of differing severity, ranging from major events, such as severe windstorms, to small events such as localized windfall. Large, severe disturbances tend to occur less frequently than small, localized ones. To capture this natural variability, we allowed four rates of disturbance in our simulation model: 0.1%, 0.5%, 1% or 5% of the forest disturbed in any one year. Because more severe disturbances occur less often, we set the frequency at which these disturbances occur at 70%, 15%, 10% and 5% respectively. That is, in 7 out of 10 years on average (70% of the time), 0.1% of the forest is disturbed each year, while a disturbance affecting 5% of the forest occurs, on average, once every 20 years (5% of the time).

There are no studies available to estimate actual annual rates of disturbance over several years (only average rates across years), and it would be entirely reasonable to consider an alternative set of annual disturbance rates and corresponding frequencies. Nevertheless, the values we have selected fit with what we know about average disturbance rates in forests. In particular, the average rate of natural canopy gap formation in forests invariably falls in the range 0.5–1.5% of forested area disturbed per year (Runkle & Yetter 1987; Lawton & Putz 1988; Stewart et al. 1991; Feener & Schupp 1998; Runkle 1998). For mountain beech trees in Kaweka Forest Park, the average annual mortality rate has been calculated at 2% per annum from re-measurement of permanent plots after 17 years (Allen & Allan 1997, pg 9; Bellingham et al. 1999). This value, however, may overestimate the long-term average because it covers the episode of severe disturbance in the 1980s, when mortality rates in Kaweka mountain beech forest appear to have been unusually high. From plots located throughout New Zealand, Wardle (1984) estimates the long-term average mortality rate of mountain beech trees to be 0.63% per annum. The annual disturbance rates and frequencies used in the simulation runs correspond to an average disturbance rate of 0.5% per annum, close to Wardle's estimate.

Starting in the year 2006 we grew the Kaweka mountain beech forest 100 years into the future. Each year we determined the amount of forest disturbed by selecting at random from one of the four annual disturbance rates, with the draw weighted by the frequency at which each rate occurs. Hence, each simulation run produces a 100 year series with a different pattern of disturbance, but all simulations have the same long-term average disturbance rate of 0.5% per annum. For each simulation we allowed the disturbed canopy openings to recover at a rate given by the recovery times we estimated under each of the three deer-control treatments. That is, in each simulation run we compared the trajectory of the forest using the recovery rates for recreational hunting, aerial hunting and fencing. We can then compare how the proportion of mountain beech forest that is in an 'open' state changes through time under each of the three deer-control treatments for a given disturbance scenario.

Figures 10, 11 and 12 show three typical examples of simulation runs.

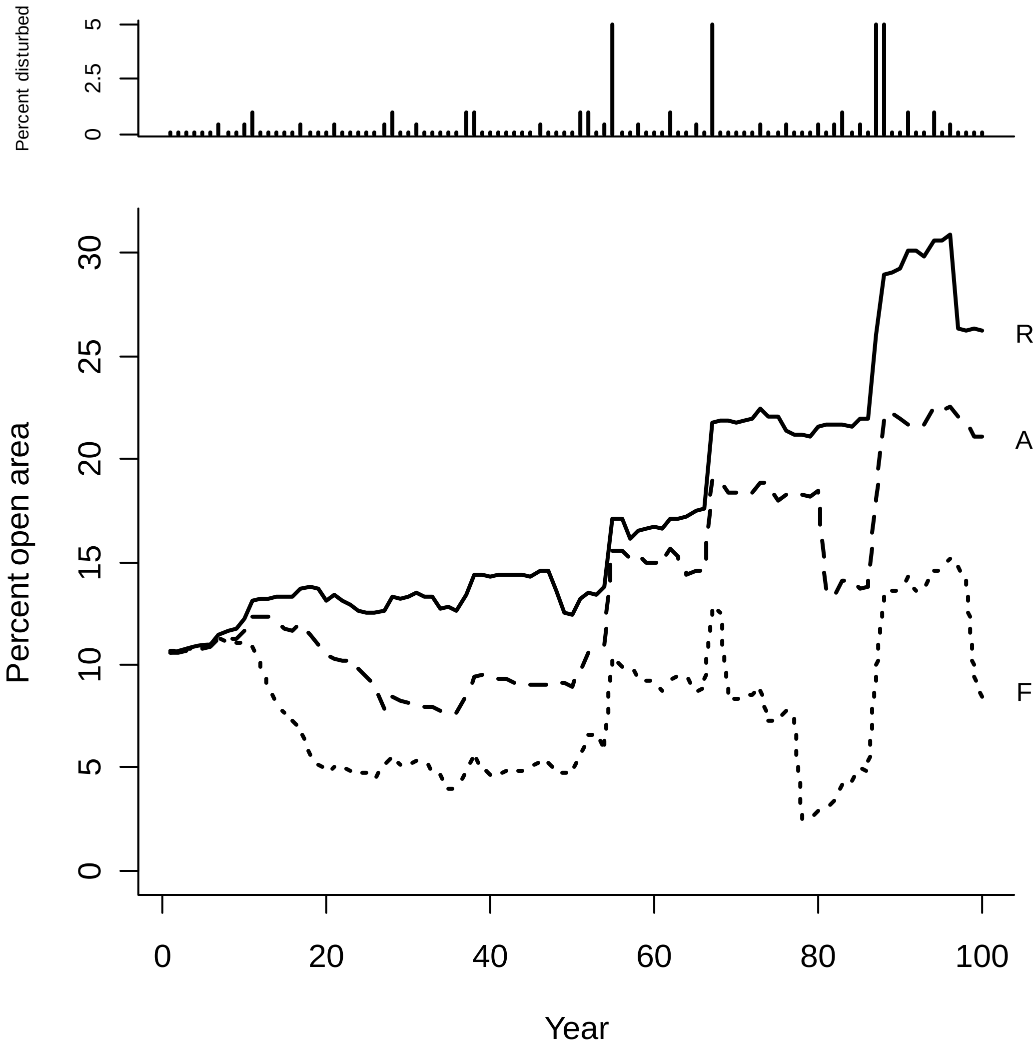

Figure 10. Result from a single 100 year run of the simulation model. The upper graph shows the percent of forest disturbed each year. The lower graph shows the corresponding amount of forest in an 'open' state under each of the three deer control treatments. R = recreational hunting, A = aerial hunting, F = fenced.

For the simulation run shown in Fig. 10, no major disturbance occurs during the first 55 years and the amount of open forest stays below 15% in all treatments. Four larger disturbances open up the forest after 55 years, with the forest remaining more open under recreational hunting due to the slower recovery rate. Recovery rates under deer exclusion (fencing) are sufficient to keep open area under 10% for most of the time.

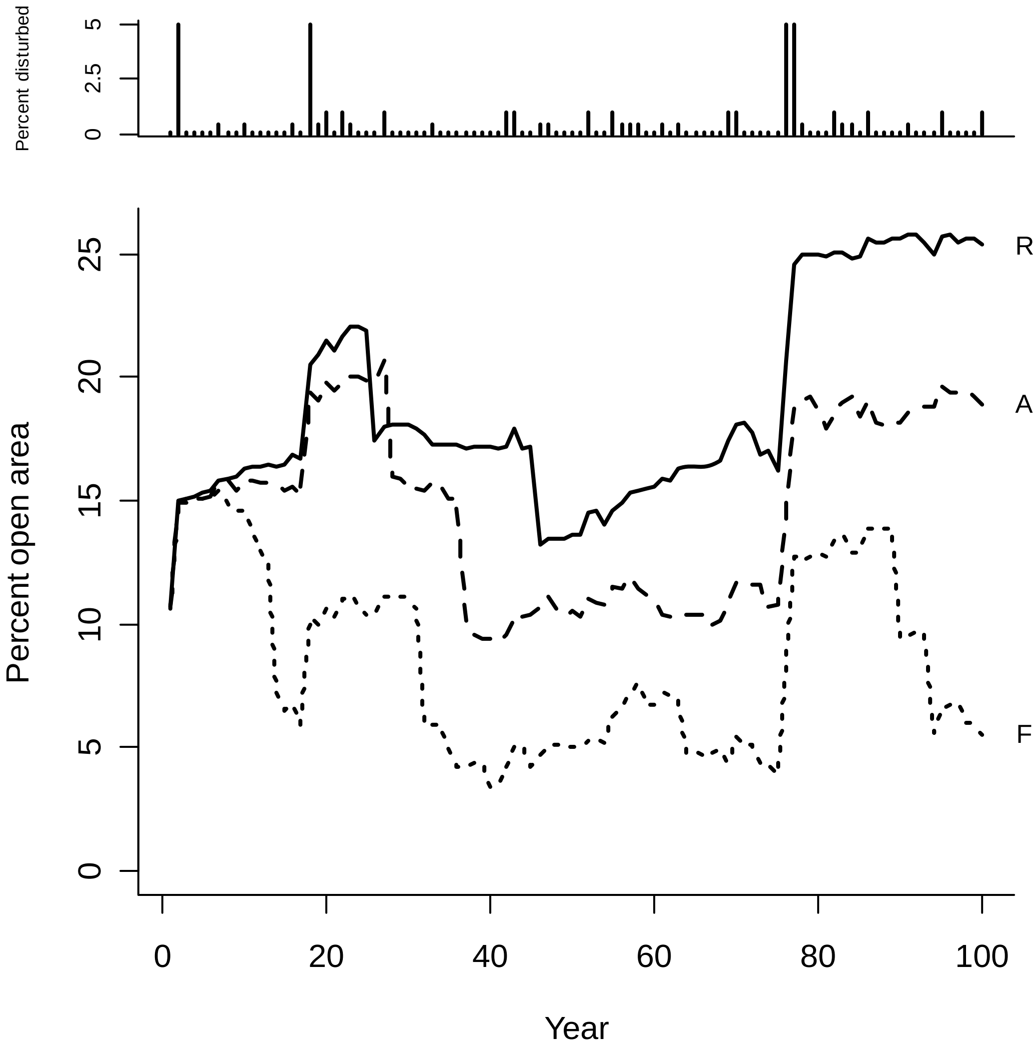

Figure 11. Result from a single 100 year run of the simulation model. The upper graph shows the percent of forest disturbed each year. The lower graph shows the corresponding amount of forest in an 'open' state under each of the three deer control treatments. R = recreational hunting, A = aerial hunting, F = fenced.

For the simulation run shown in Fig. 11, a large disturbance in year 2 and another less than 20 years later open up the forest under both recreational and aerial hunting. Over this period there is little difference between these two treatments in the amount of open area. Differences emerge, however, as the forests recover, with the slower recovery rates under recreational hunting keeping the forest more open. This difference is further evident when large disturbances again open up the forest at about 80 years. Again, despite the occurrence of disturbances that open up the forest, recovery to below 10% open area is rapid under fencing.

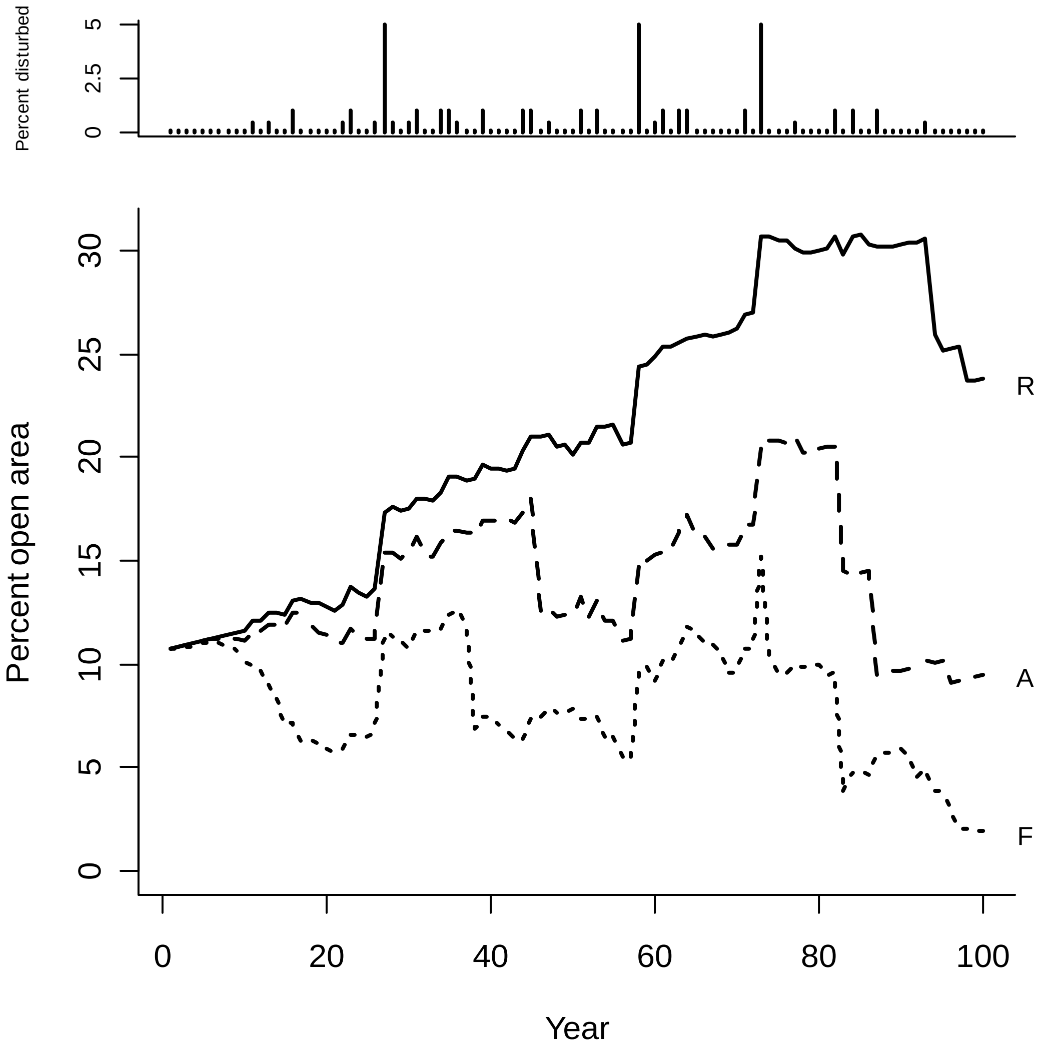

Figure 12. Result from a single 100 year run of the simulation model. The upper graph shows the percent of forest disturbed each year. The lower graph shows the corresponding amount of forest in an 'open' state under each of the three deer control treatments. R = recreational hunting, A = aerial hunting, F = fenced.

Finally, Fig. 12 shows a simulation run in which no major large disturbance occurs in the first 25 years, with the proportion of open area remaining under 15% in all treatments. Subsequent disturbances open up the forest, where it remains more open under recreational than aerial hunting. Again, under fencing the percent of open area tends to recover rapidly to below 10%.

In simulation runs, the amount of forest in an open state at any point in time results from an interplay between the pattern of natural disturbance and the deer control treatment. In certain situations, this results in little difference in the amount of open area between recreational and aerial hunting (for example, years 0-25 in Fig. 11). In other situations, it can lead to more marked differences (for example, year 100 in Fig. 12). In general, differences between the three treatments tend to become greater with time, although there are exceptions.

We can summarise the results of the simulation model by looking at the behaviour of the forest under different deer control treatments averaged over a large number of simulation runs. The resulting average trajectories do not describe how the forest is going to behave; this remains uncertain given the unpredictability in future disturbance events. What they do show is the average outcome we would expect under this disturbance scenario.

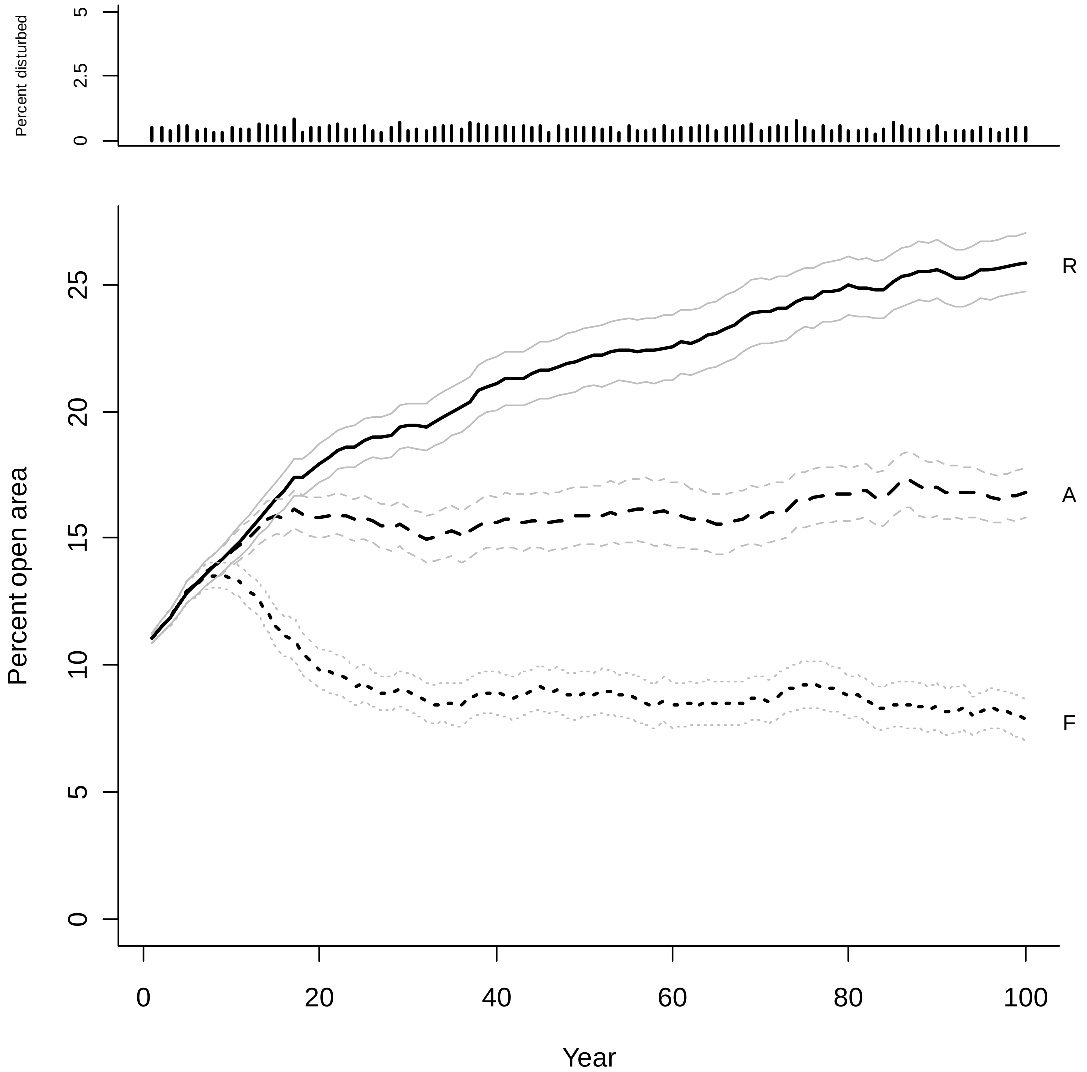

Figure 13. Averages from 100 runs of the simulation model. The upper graph shows the average percent of forest disturbed each year. The lower graph shows the corresponding average amount of forest in an 'open' state under each of the three deer control treatments, along with 95% confidence intervals around the means. R = recreational hunting, A = aerial hunting, F = fenced.

Fig. 13 shows the outcome averaged over 100 runs of the simulation model. In the upper graph the amount of forest disturbed each year averages out at 0.5%, with slight variation due to some years receiving, by chance, more large disturbances than others in the simulation runs. Under the fencing treatment, on average, open area initially increases but then declines to a mean of about 8% open area. This matches the typical proportion of *Nothofagus* forest that is in open canopy gaps in other parts of the country where deer do not appear to affect canopy regeneration (Stewart et al. 1991). In this respect they can be regarded as a 'fenced' treatment. With aerial hunting, the average proportion in open area increases then levels off at about 15%. With recreational hunting, the average proportion of open area continues to increase up to about 25% after 100 years. Hence, under this disturbance scenario (with a disturbance rate averaging 0.5% per annum), the most likely outcome of increasing the rate of recovery by switching from recreational to aerial hunting is a reduction in the amount of forest in an 'open' state by about 10% after 100 years.

The simulation model can be run using alternative disturbance scenarios to examine outcomes under different circumstances. In terms of these outcomes, the key parameter determining the average behaviour of the system in simulation runs is the average rate of disturbance. The disturbance scenario we used above has an average disturbance rate of 0.5% per annum, close to the average annual mortality rate calculated for mountain beech (Wardle 1984). This therefore represents a highly plausible scenario. We also ran the simulation model using three other average rates (Table 2), covering the range typically observed in forests.

Table 2. Relationship between annual rate of disturbance and benefit gained by aerial hunting measured as the area of forest in an 'open' state after 100 years (each figure is the average from 100 simulation runs)

Average annual disturbance rate (%)	Reduction in the mean proportion of forest in an 'open' state by switching from recreational to aerial hunting after 100 years (%)
0.5	10
1	15
1.5	18
2	19

Hence, under a range of rates that encompass the typical background rates at which disturbances form canopy openings, increasing the rate of recovery by switching from recreational to aerial hunting would, in the long term, reduce the amount of mountain beech forest in an 'open' state by about 10–20%.

4.2 SPECIES COMPOSITION CONSEQUENCES

We may also expect community-level consequences of the delay in forest recovery at a range of scales.

4.2.1 Below-ground

Browsing of individual seedlings likely has consequences for a range of associated above- and below-ground biota. For example, it appears herbivores commonly have a negative effect on the levels of mycorrhiza found on plant roots (Gehring & Whitham 1994). We know mycorrhiza are critical to beech seedling performance. As a result, the slow growth of individual seedlings exposed to deer browsing outside the fences could be a consequence of indirect effects (e.g. through mycorrhiza) of browsing on the seedlings in addition to growth consumption alone.

4.2.2 Shrub communities

In some parts of the open-canopied mountain beech forests shrubby plants dominate; elsewhere it has been found such woody vegetation assists mountain beech to regenerate in open areas (Ledgard & Davis 2004). It is unclear how a delay in beech recovery will influence shrubby areas.

4.2.3 Turf communities

In contrast, in other parts of the Kaweka mountain beech forests, browsing by sika deer appears to have induced and maintained a browse-tolerant, turf-forming community of herbs, ferns and bryophytes in open areas (cf. Husheer et al. 2006a). Based upon an experimental removal of these turf communities in the nearby Kaimanawa Range it has been shown that planted and naturally occurring mountain beech seedlings respond with increased growth and survivorship (Husheer et al. 2006a). However, fencing of turf communities to exclude deer in the Kaimanawa Range by Husheer et al. (2006a) did not lead to a compositional response by the turf within 3 years. This suggests relatively rapid seedling growth in Kaweka Forest Park fenced areas was not partly a consequence of changes in local turf competition. Also, it is noted that any deer-induced changes in forest understories are not necessarily reversible by removing the herbivore involved (Coomes et al. 2003). Whatever the cause of these turfs it has been shown elsewhere that such herbaceous communities limit the early stages of mountain beech establishment (e.g. Ledgard & Davis 2004; Husheer et al. 2006a). One mechanism is that these turf communities transpire less water than trees and result in higher soil water content and in some instances water logging that limits beech establishment. Another mechanism limiting beech recruitment is that such turf communities are dominated by arbuscular mycorrhiza in the soil and these are unsuitable for mountain beech establishment as beech require ectomycorrhizas. A plausible consequence of the delay in recovery of mountain beech, in areas subjected to recreational hunting, is the maintenance of these light-demanding turf communities, and their associated biota, because they will not be shaded out by canopy closure. However, one reason to suspect that these turf communities are not ultimately limiting beech recruitment over the period of measurements is that with fencing all plots rapidly recovered enough individuals to replace and maintain the canopy.

4.2.4 Invasive weeds

Disturbed areas, such as those in mountain beech forest having an open canopy, often contain exotic light-demanding weedy plants. In Kaweka Forest Park a number of exotic herbs and grasses are found in the open (<44 m^2/ha) forest (from National Vegetation Survey Databank). As a consequence, we would expect a delay in forest recovery to allow the longer persistence of weedy species and greater opportunities for seed production. If, as our simulations suggest, Kaweka Forest Park mountain beech forests would develop more open areas under recreational hunting than the other two hunting regimes, we would expect a more general distribution of exotic weedy species and a greater ability of readily dispersed exotic species to maintain viable populations.

4.3 ECOSYSTEM DYNAMIC CONSEQUENCES

Because mountain beech is the structural dominant in the forests studied, forest development (the aging of open forest) itself will influence a wide range of ecosystem properties through time. This includes how the pools and fluxes of energy and nutrients change as forest ages.

4.3.1 Nitrogen

For example, Fig. 14 depicts how soil-available nitrogen (mineralisable N), foliage N concentration, and the N stored in tree stemwood and coarse woody debris change as a mountain beech forest develops in the Craigieburn Range (from Clinton et al. 2002). We would expect a similar pattern in Kaweka mountain beech forests. The open forest we studied recovery of in Kaweka Forest Park represents development between the 'Seedling' stage and the 'Sapling' stage in Fig. 14. What we see between these stages is increasing N stored in the stemwood as tree biomass increases, decreasing N stored in the woody debris (CWD) as logs decompose, and an increase in soil N availability.

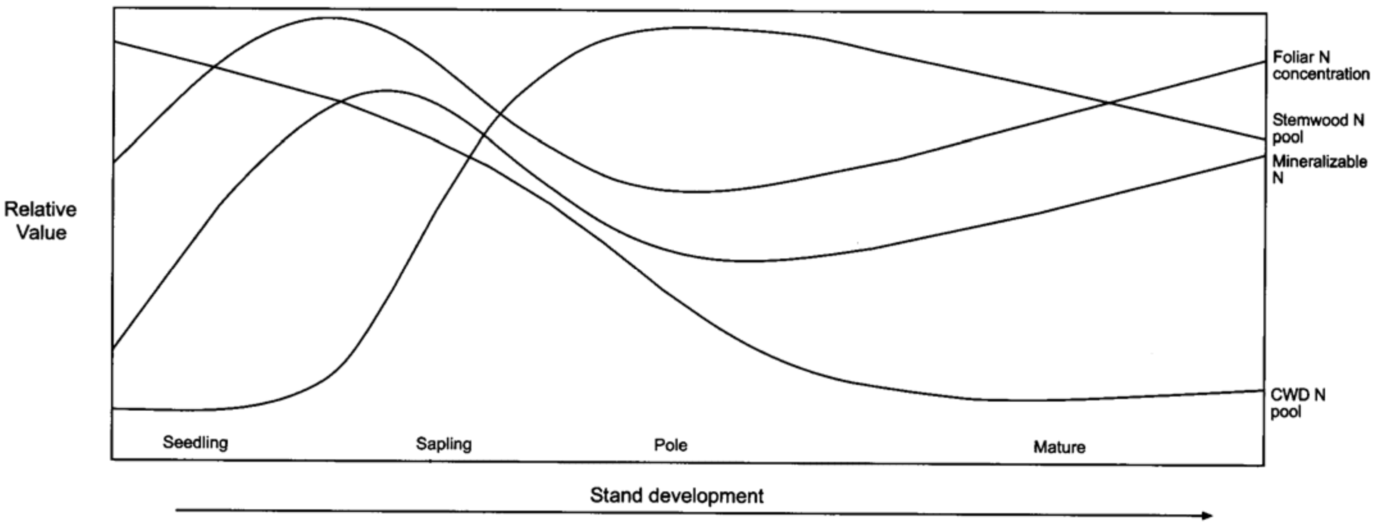

Figure 14. Nitrogen pools in a mountain beech forest during stand development. From Clinton et al. (2002).

What then is the consequence of slower canopy recovery in Kaweka Forest Park when deer browse on regenerating tree seedlings? The woody debris will continue to decompose and eventually release N, the availability of N will thus increase in the soil, but reduced uptake and storage in the slower-accumulating stemwood may further elevate available N in the soil. Available N in the soil is mobile and can be leached from the soil in waterways. As a consequence, there is a possibility of loosing some of this growth-limiting nutrient from the soil with a delay in recovery.

Similar relationships exist for other key nutrients:
- Cations (see Allen et al. 1997)
- Phosphorus (Brandtberg pers. comm.)

4.3.2 Carbon

Davis et al. (2003) show that carbon storage in developing mountain beech forest in the Craigieburn Range declines between the seedling and sapling stages because the loss of carbon to the atmosphere from woody debris exceeds that accumulated in the increasing tree biomass. There is relatively little change in the soil carbon pools. So the increase in forest recovery time from fencing to aerial hunting to recreational hunting likely equates to a greater decline in the amount of carbon stored. Our simulations show an increasing proportion of area in open forest from fenced to aerially hunted and to recreationally hunted areas respectively. For the mountain beech forests of Kaweka Forest Park as a whole this equates to most carbon stored in fenced forest and least in recreationally hunted forest. We have not calculated the absolute levels of carbon storage but suggest this will eventually have a direct financial cost to the country under our carbon emission reporting obligations. This becomes more sobering as sika deer spread into adjacent forests and apparently lead to similar limitations to forest recruitment (e.g. Husheer et al. 2006b).

4.3.3 Nutrient cycling

Browsing also influences a wider range of organisms than just the structural dominant, with flow on effects to ecosystem processes. Wardle et al. (2001) have demonstrated significant effects of browsing mammals on plant species composition, litter layer composition, and species composition of various litter-dwelling faunal groups throughout New Zealand indigenous forests. In a general sense, fenced areas should have more plants producing palatable, high-quality, decomposable litter and fewer plants producing unpalatable and low-quality litter. The study of Wardle et al. (2001) also showed browsing mammals significantly influenced soil C and N storage on an areal basis for some types of forest. While the direction of a herbivore effect on these compositional and nutrient-storage properties was often inconsistent, the results do suggest fencing in Kaweka Forest Park will cause responses in these properties that are different to those found under the other hunting regimes.

4.4 IS THERE EVIDENCE THAT AERIAL HUNTING PROMOTED THE RECOVERY OF UNDERSTOREY SPECIES?

The 189 mountain beech plots sampled in 2005/06 covered areas that had a history of aerial hunting and areas that had only received recreational hunting. To test whether a history of aerial hunting had resulted in an increase in the abundance of species other than mountain beech, DOC staff counted seedlings of four common understorey species: *Coprosma pseudocuneata*, *C. foetidissima*, *Griselinia littoralis* and *Raukaua simplex*. The number of seedlings >15 cm and <135 cm for each species was summed per plot and these values were used to calculate the mean number of seedlings per plot (and 95% confidence intervals) under different deer control treatments (aerial and recreational hunting; Fig. 15). For all four species, the 95% confidence intervals around the means for each treatment overlapped, implying there was no significant difference in the density of these species between treatments.

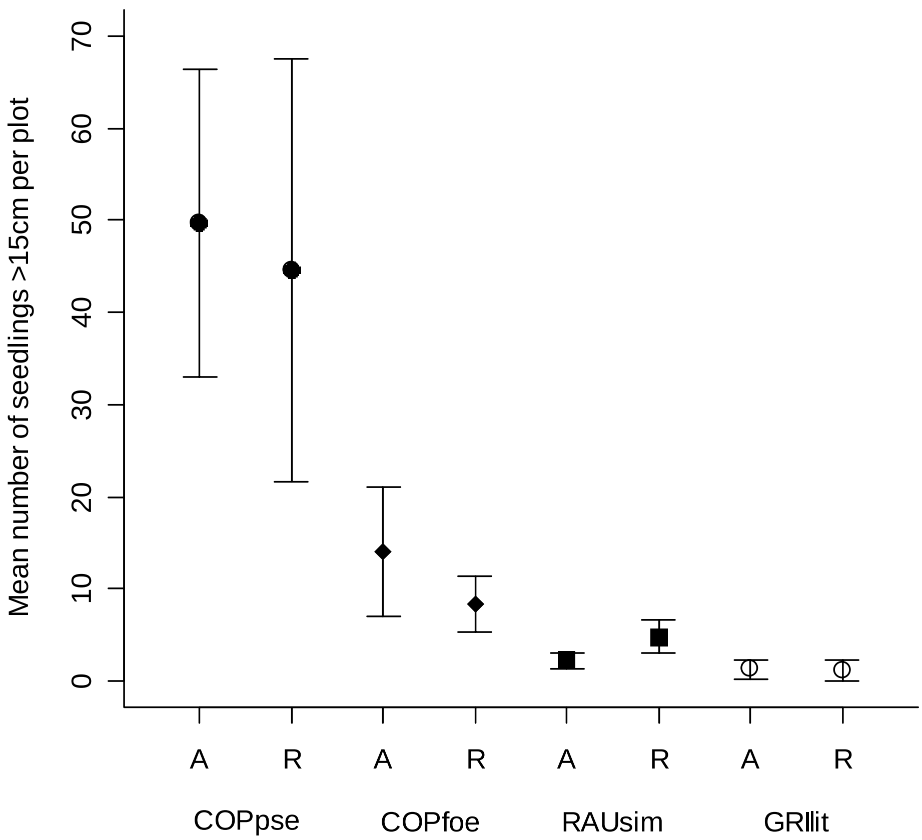

Figure 15. Mean number of seedlings >15 cm tall per plot (and 95% confidence intervals) for four understorey species (*Coprosma pseudocuneata*, *C. foetidissima*, *Raukaua simplex* and *Griselinia littoralis*) common to mountain beech forest in areas that received aerial (A) or recreational (R) hunting treatments.

5. Summary

- The tagged seedling data from 1997 to 2004 enabled us to model seedling growth, recruitment and survival.
- On average, mountain beech seedlings grew fastest in fenced plots and slowest in plots under recreational hunting.
- The 2005/06 systematic survey of the Kaweka mountain beech forest using 189 plots included 29 plots that had a basal area <44 m^2/ha of which 20 had insufficient saplings for canopy recovery. Canopy recovery on these 20 plots under three deer-management treatments was modelled using growth, survival and recruitment models developed from tagged seedlings.
- Regardless of the treatment applied there was always substantial variation among plots in their recovery time.
- Adequate recovery is achieved most rapidly with fencing and least rapidly with recreational hunting, with aerial hunting intermediate.
- The time taken for a plot to recover was related to initial seedling density; plots with few seedlings took longest to recover.
- The time taken for plots to recover under the three deer management treatments was applied to a simulation model of disturbance dynamics over 100 years. The long-term outcome of the model suggested that the continued presence of deer will result in an increase in the amount of open forest. This increase is greatest under recreational hunting and could be reduced by aerial hunting.
- We expect an increase in open forest will have consequences for ecosystem properties, including live tree biomass and carbon storage.

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