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A tree hollow dynamics simulation model

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Abstract

This paper describes a deterministic computer model for simulating forest dynamics. The model predicts the long-term dynamics of hollow-bearing trees which occur in a single-species (monotypic) forest stand under an array of different timber harvesting regimes over a time scale of centuries. It is applied to a number of different timber harvesting scenarios in the mountain ash (*Eucalyptus regnans* F. Muell.) forests of Victoria, south-eastern Australia. Computer experiments give results that have far-reaching implications for forest management and could not have easily been predicted without a model. These include: (1) when the harvest rotation time is 100 years or less, a supply of trees with hollows cannot be ensured by only retaining trees which already have hollows: and (2) when some retained trees are lost through logging-related mortality, the effect on the number of trees with hollows is exaggerated. For instance, if half of the retained trees are lost via logging-related mortality, it is not sufficient to double the number of trees retained in order to maintain the same number of hollow-bearing trees.

HOLSIM is a planning tool for forest and wildlife managers. it will assist them in forecasting long-term stand conditions that result from particular forest management regimes. The ability to make predictions over several harvesting cycles is extremely important for examining the effects of harvesting strategies on the dynamics and structure of forest ecosystems, determining if given management strategies will meet particular targets, anticipating the impacts of forestry operations on hollow-dependent fauna, and helping to better integrate biodiversity conservation within wood production forests.

Keywords: Forest ecosystems; Forest management; Hollows; Cavities

1. Introduction

The potential impacts of timber harvesting operations on the conservation of biodiversity has become a major planning and policy issue in the management of Australian wood production eucalypt forests (Resource Assessment Commission, 1992; The Commonwealth of Australia, 1992; Department of the Environment, Sports and Territories, 1995). Of the many species that inhabit wood production forests, those that use hollows in trees are considered to be amongst those most vulnerable to the impacts of timber harvesting (McIlroy, 1978; Recher et al., 1980; Lindenmayer et al., 1990a, b; Scotts, 1991; Gibbons and Lindenmayer, 1996). This is because

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hollows suitable for occupation by wildlife may take several hundred years to develop (Ambrose, 1982; Saunders et al., 1982; Lindenmayer et al., 1991c, 1993; Gibbons, 1994) and the type of logging operations used, as well as the interval between harvesting events, may prevent or severely impair the recruitment of such trees (Lindenmayer et al., 1990b; Recher, 1996; Gibbons and Lindenmayer, 1996). This will have a negative effect on the large number of vertebrate and invertebrate taxa that are obligate or facultative hollow-using species (Gibbons and Lindenmayer, 1996). As hollow development in Australian eucalypt trees takes a long time, rectifying hollow shortages in wood-production forests will take a long time as well (Lindenmayer and Possingham, 1995; Recher, 1996). Trees with hollows are a characteristic component of forest ecosystems, not only in Australia (Scotts, 1991; Lindenmayer et al., 1993) but in many places around the world (Newton, 1994). They are a key habitat component for a wide array of vertebrate and invertebrate taxa (Gibbons and Lindenmayer, 1996) and provide nesting and denning sites as well as places for animals to roost and perch (Lindenmayer and Franklin, 1998).

Tree retention strategies can help avoid hollow shortages and mitigate the impact of logging on hollow-dependent fauna. For example, studies of a range of different types of eucalypt forest have highlighted the value of retained trees in facilitating the recolonisation of logged sites by birds (Loyn et al., 1980; Recher et al., 1980; Smith, 1985; Kavanagh and Turner, 1994). However, the long-term effectiveness of tree retention strategies remains unknown (Gibbons and Lindenmayer, 1996). The long-term nature of hollow dynamics makes it extremely difficult to assess the efficacy of tree retention strategies in the field. It also means that it is extremely difficult for forest and wildlife managers to forecast the stand conditions which will occur well into the future as a result of the management actions taken now. The long-term dynamics of hollows in a forest stand are considerably longer than the careers of professional foresters and wildlife managers. Hence, individuals are unlikely to observe the long-term consequences of a given management action, or easily comprehend the full effects of their activities. This makes it difficult for forest managers to track and/or visualise the long-term changes in forest architecture, particularly relating to tree hollows, that can be associated with particular management actions, without the aid of forest models.

Given the difficulty of predicting the impact of harvesting on hollow dynamics, we developed HOLSIM, a computer-simulation Markovian model that explores and forecasts the long-term changes in stand structure which result from the implementation of different management actions and tree retention strategies. The model is different from many other stand models that have been developed because it is focussed on the development of hollows and simulates forest conditions well after growth rates have peaked and trees have entered prolonged periods of senescence. The model is of interest from a modelling perspective, because its structure is determined by the data that is available or readily obtainable, and the questions of interest to the manager. For example, stand development is modelled in a phenomenological fashion, ignoring key driving processes like water, light, and nutrients. This is because data on the influences of these processes on the long-term growth of trees and formation of hollows is rare or nonexistent for most tree species.

A number of user-related issues were taken into account in developing HOLSIM:

- It should be applicable to forests where there are limited data on hollow ontogeny.
- The model has to allow a wide array of management actions.
- It has to be able to simulate a long time scale.
- It has to be able to run on a personal computer in reasonable time in order to be used as an exploratory forest manager tool.

Mountain ash typically occurs as a single species stand (Ashton, 1976), making it inappropriate to use any of the many forest succession models (see, for example Acevedo et al., 1996; Lin et al., 1996; Osho, 1996). The general lack of knowledge about stand dynamics (particularly the mechanisms of hollow ontogeny over long time scales) made it inappropriate to use existing generic vegetation models based on ecological mechanisms, such as VAFS/STANDSIM (Roberts, 1996), TREEDYN3 (Bossel, 1996), or other descendants of JABOWA (Botkin et al., 1972) and FORET (Shugart, 1984).

The model was tested with a number of different timber harvesting scenarios in the mountain ash

Table 1
Some studies completed on the ecology of mountain ash forests and associated vertebrate fauna in the Central Highlands of Victoria (modified from Lindenmayer and Franklin, 1998)

Type of study	References
Stand growth and development	Dahl (1940); Cunningham (1960); Ashton, 1975a, b, c; Ashton, 1976; Ashton, 1981)
Spatial and temporal variation in forest structure	(Ashton, 1975a, b, c; Ashton, 1976; Ashton, 1981); Adams and Attiwill (1984); (Lindenmayer et al., 1990d; Lindenmayer et al., 1991a)
Stand longevity and dendrochronology	Ambrose (1982); Banks (1993)
Hollow ontogenty	Ambrose (1982); Lindenmayer et al. (1993)
Impacts of logging on stand structure	(Lindenmayer et al., 1990a, b, c; Lindenmayer, 1992a; Lindenmayer et al., 1994); Ough and Ross (1992)
Impacts of logging on wildlife	(Smith and Lindenmayer, 1988, 1992); (Lindenmayer, 1989, 1992b, 1994, 1995); Lindenmayer et al. (1990b); Lindenmayer and Possingham (1995)

(*Eucalyptus regnans* F. Muell.) forests of Victoria, south-eastern Australia. It was parameterised using information generated from past studies of mountain ash forests (see Table 1) including: rates of stand growth (Dahl, 1940; Cunningham, 1960; Ashton, 1975a, b, c, 1976, 1981), typical stocking rates of trees (Burgman et al., 1995; Ambrose, 1982; Banks, 1993), patterns of cavity ontogeny (Ambrose, 1982; Lindenmayer et al., 1993), and patterns of decay and collapse among hollow-bearing stems (Lindenmayer et al., 1990a, 1997).

The model is generic and can be parameterised for use in forest types characterised by different life-history attributes and different management regimes. Input data needed to run the model include:

- a transition matrix of the movement of trees through various growth stages (i.e. tree forms);
- patterns of cavity ontogeny, such as the time required for stems to begin to develop hollows;
- the rates of tree growth;
- tree density in stands of different ages; and
- rates of mortality of trees retained on logged sites.

2. The model

2.1. Model structure

HOLSIM models a single-species (monotypic) forest stand and simulates the composition of the forest with respect to the size and life stage of the trees. We assume that the number of hollows is only a function of tree size and form and that, by modelling the dynamics of the trees in a stand, we can predict the dynamics of the number of hollow-bearing trees. In this study, we use a default stand area of 25 ha. The location of individual trees and the spatial distribution of classes of trees within the stand is not included in the model. For this reason the stand area is simply a scaling parameter which can be set to any area.

The length of the time step used in the simulation can be varied; we used a time step of five years. In each time step, the forest changes through a series of processes, each of which is described below. These processes are: growing the trees; computing the decay of healthy trees; recruitment of new trees; tree death; the decay of damaged trees; and changes to a stand associated with timber harvesting operations. The programme does not allow for any catastrophes (e.g. wildfires or storms) or long-term environmental changes, and is completely deterministic.

For the purposes of this study, we assumed recruitment in mountain ash forests only occurs after a disturbance (logging), at which point new trees fill all the available space from the seed bank. Stands of mountain ash regenerate well after disturbances like wildfire and logging (Attiwill, 1994). Because the only disturbance allowed in the simulations is logging, a simulation without logging would be unrealistic as we have little information about the dynamics of this species when there is no disturbance for hundreds of years [Therefore, scenarios without the effects of timber harvesting were not pursued.]

2.2. Forest structure and tree growth

Trees are categorised into states determined by size and condition. Because HOLSIM is a deterministic

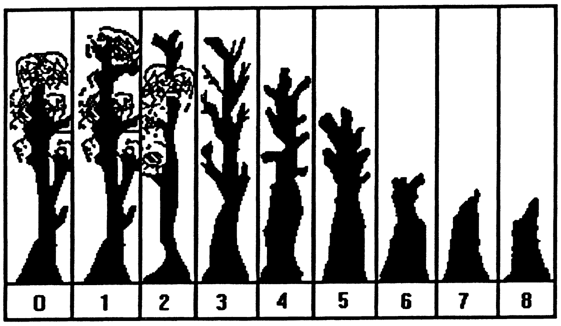

Fig. 1. Tree forms 0–8. Tree Form 0 is a living tree which has not formed any hollows; Form 1 is a mature living tree with hollows; Form 2, mature living tree with a dead or broken top; Form 3, dead tree with most branches still intact; Form 4, dead tree with 0–25% of top broken off, branches remaining as stubs only; Form 5, dead tree with top 25–50% broken away; Form 6, dead tree with top 50–75% broken away; Form 7, solid dead tree with $\geq$75% of the top broken away; Form 8, hollow stump. (Modified from Smith and Lindenmayer, 1988).

model, the number of trees in each state is the expected or average number of trees for that state. They are the average which occur over a number of stochastic simulations based on the same parameters.

Each tree in the forest has two defining attributes: (1) its size class; and (2) its form, which is a measure of its condition, or life stage (see Fig. 1). The size-class category represents the size of the trees. There are 50 distinct size classes, where the largest size class contains mature trees of $\approx$250 years of age as well as trees older than this. It is scaled so that a healthy tree (one unaffected by decay and with no hollows) will increase on average one size class in each time step (5 years). Before decay begins, the age of the tree will roughly be its size class times the length of a time step. The relationship between the average diameter at breast height (DBH) of a size class and the average age of the size class is calculated by a formula given by Ashton (1976):

$$Y = X^{1.02}, \quad (1)$$

where Y is the DBH in centimetres and X the age in years.

The form of a tree ranges from zero to eight, reflecting advancing stages of senescence (Fig. 1). The forms are defined as follows (after Smith and Lindenmayer, 1988):

- Form 0, living tree without hollows;
- Form 1, mature living tree with hollows;
- Form 2, mature living tree with a dead or broken top;
- Form 3, dead tree with most branches still intact;
- Form 4, dead tree with 0–25% of the top broken off, branches remaining as stubs only;
- Form 5, dead tree with the top 25–50% broken away;
- Form 6, dead tree with the top 50–75% broken away;
- Form 7, solid dead tree with $\geq$75% of the top broken away; and
- Form 8, hollow stump.

2.3. Transition processes

During each time step, the distribution of trees in the forest changes through a series of transition processes. The transition processes cause a fraction of trees in each state to flow into a variety of other states. These processes include: senescence (using the form transition matrix shown in Table 2 adapted from Lindenmayer et al., 1998), mortality through overcrowding, density-independent mortality, growth, recruitment, and harvesting. The processes that cause trees to change state are summarised in Fig. 2 and described in the following.

2.4. Senescence and changing tree form

Senescence is the first process applied in each time step. It includes the senescence of already damaged trees (tree forms 1–8) and density-independent mortality (the mortality of healthy trees which is not caused by overcrowding) (see Fig. 3). These transitions are independent of the composition of the forest in the model.

Mature trees (at or above size class 18) can form hollows and, hence, be transferred from tree Form 0 to tree Form 1 (mature living trees with hollows). The rate at which they move is a linear function of stem basal area and, hence, a quadratic function of size class. No trees form hollows at size class 18 and 5% of trees form them at size class 50 in any given time step. This value was estimated by calibrating the model with actual forests of known age (Lindenmayer et al., 1993).

Trees which are already higher than tree Form 0 have started the decay process and a form transition matrix (Table 2) is used. It was derived from data on

Table 2
Transition frequency matrix. (Adapted from Lindenmayer et al. (1997)). The numbers are the proportion of trees of the row's tree form which are transferred into the column's tree form at each time step

Old	New								Removed
	Form 1	Form 2	Form 3	Form 4	Form 5	Form 6	Form 7	Form 8	
Form 0	0	0	0.01	0	0	0	0	0	0
Form 1	0.99	0.01	0	0	0	0	0	0	0
Form 2	0	0.87	0	0.02	0.04	0.02	0	0	0.06
Form 3	0	0	0.21	0.43	0.21	0	0	0.07	0.07
Form 4	0	0	0	0.38	0.29	0.07	0.09	0.02	0.16
Form 5	0	0	0	0	0.53	0.26	0.11	0.03	0.08
Form 6	0	0	0	0	0	0.29	0.22	0.2	0.3
Form 7	0	0	0	0	0	0	0.43	0.36	0.21
Form 8	0	0	0	0	0	0	0	0.58	0.42

the change in condition of >2000 mountain ash trees between 1983 and 1993 (Lindenmayer et al., 1998). The form-transition matrix is applied to the trees in forms 1–8 in each size class. The transition frequencies are not dependent on the size classes of the trees; the form of a tree can only increase.

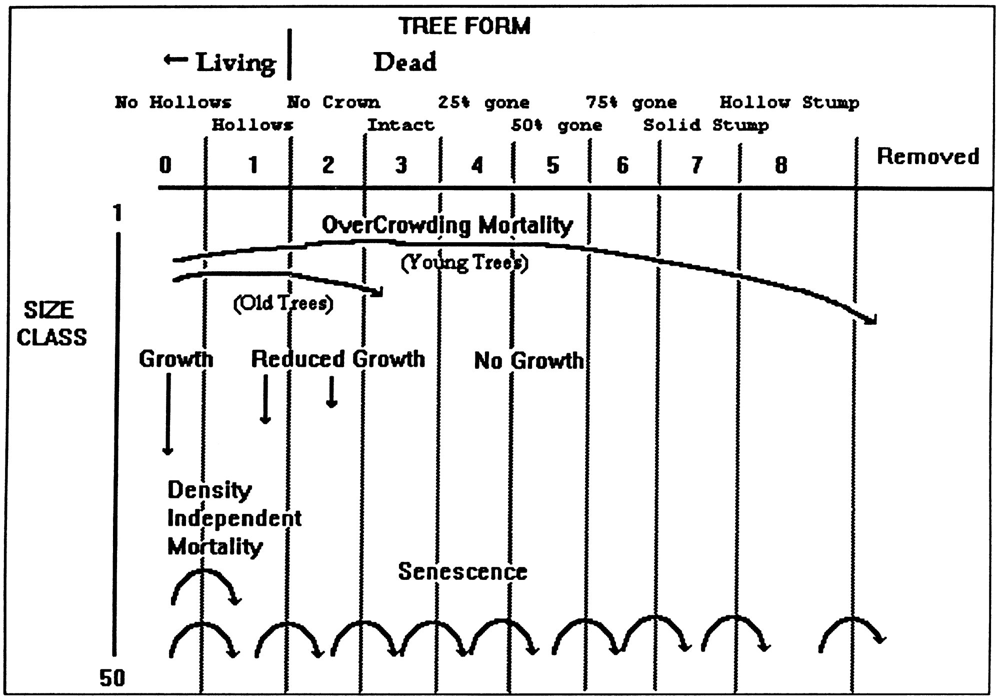

Fig. 2. Schematic diagram of transition processes. Trees are divided into size classes from 1 to 50 and tree forms from 0 to 8. The main processes are: overcrowding mortality which transfers trees into tree Form 3 (dead trees with most branches intact, see Fig. 1) or removes them from the system; growth increases the size class of trees and growth at a reduced rate increases trees of forms 1 and 2 (living trees with hollows and those with missing crown); density-independent mortality moves trees from Form 0 to Form 1 (living trees without hollows to those with missing crown); density-independent mortality moves trees from Form 0 to Form 1 (living trees without hollows to those with hollows); senescence is the general process which increases the forms of trees until they eventually collapse and are removed from the system. Note that mortality and senescence moves trees to the right and growth moves trees downwards – the only two valid directions.

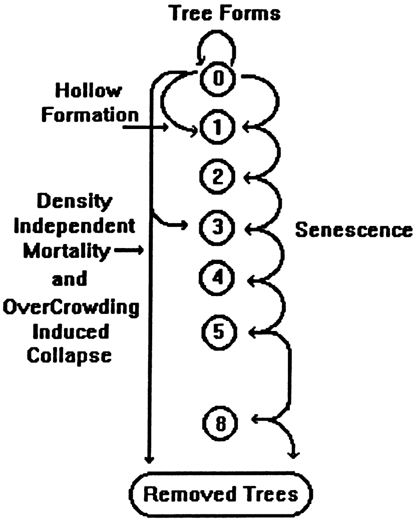

Fig. 3. Senescence processes. This is a subsection of Fig. 2. All trees start in tree Form 0 and will increase their tree form until they are eventually removed. Hollow formation moves trees from Form 0 (living with no hollows) to Form 1 (living with hollows). Overcrowding either removes trees completely (through immediate collapse) or transfers them to Form 3 (dead trees with most branches intact). All these processes are also shown in Fig. 3.

Density-independent mortality affects living trees (tree forms 0, 1 and 2). Trees below a cut-off size class collapse when they die through self-thinning (Ashton, 1981) or density-independent mortality and are removed from the simulation. Trees at, or above, the cut-off size class will die, but not immediately collapse. These trees are placed into tree Form 3 (dead trees with most branches intact, see Fig. 1). The cut-off size class, namely the size class below which trees immediately collapse, has been set at 18 which corresponds to trees ≈90 years old. This means that trees dying before this size class will not become hollow-bearing stems (based on the work by Ambrose, 1982). The rate of density-independent mortality is 1% of trees in Form 0 (living stems with, and without, hollows) as illustrated in the transition-frequency matrix given in Table 2.

2.5. Growth

The model is parameterised using information on the rate of growth in mountain ash gathered by Ashton (1976). Living trees (tree forms 1, 1 and 2) grow at each time step. It is possible for a tree to stay in the same size class in a time step or to increase either one, two, or three size classes in a single time step. It is not possible for a tree to grow more than three size classes, which would be a faster rate of growth than is known to occur in mountain ash. In addition, it is not possible for the size class of a tree to decrease. The proportion of trees of forms 0, 1 and 2, which move to the different size classes, is shown in Fig. 4. This is based upon a normal curve with a mean of one size class and a standard deviation of 0.25 size classes. The rates of

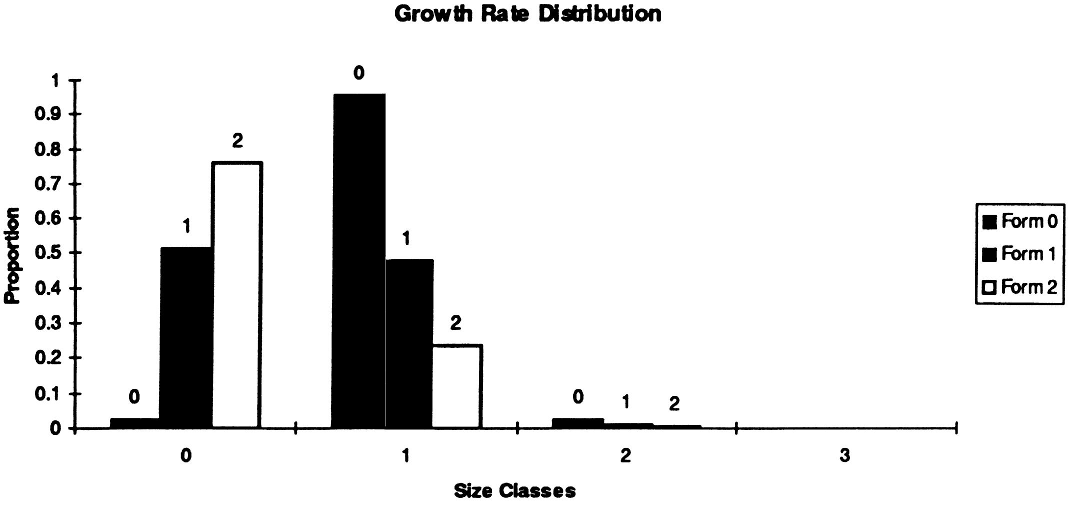

Fig. 4. Growth rate distribution. The proportion of trees (of different tree forms) that increase 0, 1 or 2 size classes in each time step.

growth of trees in tree forms 1 and 2 are less than the rate of growth of trees of Form 0.

Deriving the growth parameters for this model from observations of a forest is not straightforward. Trees which grow faster than average will become the dominant trees in an even-aged stand and, hence, have a higher survival probability. Those which grow more slowly tend to be 'crowded out' and collapse, and hence will not be observed. For this reason, it is necessary to calibrate the growth parameters to agree with observed forests. In this study, the standard deviation for growth of Form 0 trees was estimated using field information from Lindenmayer (unpublished data) to create realistic dynamics. The standard deviation was adjusted so that the forest stand would be similar in age structure to actual forest stands.

2.6. *Crowding, recruitment, and self-thinning*

'Crowding' is a term used to describe the number and size of trees in a stand. The level of crowding of trees in the forest is computed for the purposes of calculating self-thinning and, when appropriate, recruitment. It is assumed that each tree in each state uses a particular amount of some limiting resource, such as space, light, or water. By assuming that limiting resources are a linear function of space, measures of the availability of space can be used to calculate the rate of self-thinning, without loss of generality or the need to specify exactly which resource is limiting. When the amount of a resource that trees are using is greater than the available resources, the stand is overcrowded.

Ashton (1976) included a general formula for the maximum stocking of a plot. It is given as a function of tree species and size and follows a general form from Dahl (1940). Once an initial measure is taken from an even-aged stand of a given tree species, it is possible to determine the relative space required by trees of that species for all sizes. The formula for the number of possible trees of mountain ash of a given size is

$$N = \frac{e^{K}}{D^{1.605}}. \tag{2}$$

where D is the diameter, measured at breast height (DBH), of a tree in centimetres, N the maximum number of trees of the given DBH per hectare and K a species-dependent parameter. For mountain ash, K is 9.2633 (from Ashton (1976)).

The inverse of N is the amount of space a tree of diameter D requires, $S(D)$ (in hectares)

$$S(D) = e^{-K} D^{1.605}, \tag{3}$$

where $S(D)$ is the space, in ha, each tree requires. For example, $S = 0.051$ ha for a D of 50 cm and $S = 0.154$ ha for a tree diameters of 1 m. The relationship between the number of trees per hectare for different diameters is shown in Fig. 5(a). Without specifying the limiting resource, it is impossible to calculate how much of the resource is used by trees in various states of decay. For the purposes of this study, tree forms 1–8 use, or prevent other trees from using, progressively less of the limiting resource. For example, we assumed a Form 5 tree uses 20% of the resource required by a Form 0 tree of the same diameter. The values used in this study are displayed in Fig. 5(b). When the ratio of decayed to healthy trees is high and the forest is near or at its maximum crowding, then errors in the estimation of resource use by these damaged and dead trees may be significant. However, this situation rarely occurs in our model.

Overcrowding can occur after the growth phase of stand development and initiates the self-thinning phase. In self-thinning, trees are removed (i.e. collapse or die) from the forest until the stand is no longer overcrowded. Trees of the smallest size class are removed first, followed by the next smallest, and so on. Trees in size class 18 or higher might not immediately collapse, but might be transferred to tree Form 3 (dead trees with most branches still intact, see Fig. 1). The frequency with which these trees will be transferred to tree Form 3 rather than collapsing is based upon a quadratic function of the tree's size class. [Hence, it is approximately linearly dependent on the basal area of the trees.] The function is set so that trees in size class 18 or lower have a 100% chance of collapsing and 100% of trees in size class 50 will remain standing in Form 3 after they die through overcrowding. When overcrowding effects trees in larger size classes, trees in Form 2 will be the first ones transferred to tree Form 3 followed by Form 1 trees and then those in Form 0, until the forest is no longer overcrowded.

Recruitment generally occurs in mountain ash only after a disturbance (Attiwill, 1994). The only source of disturbance in this model is timber harvesting, because

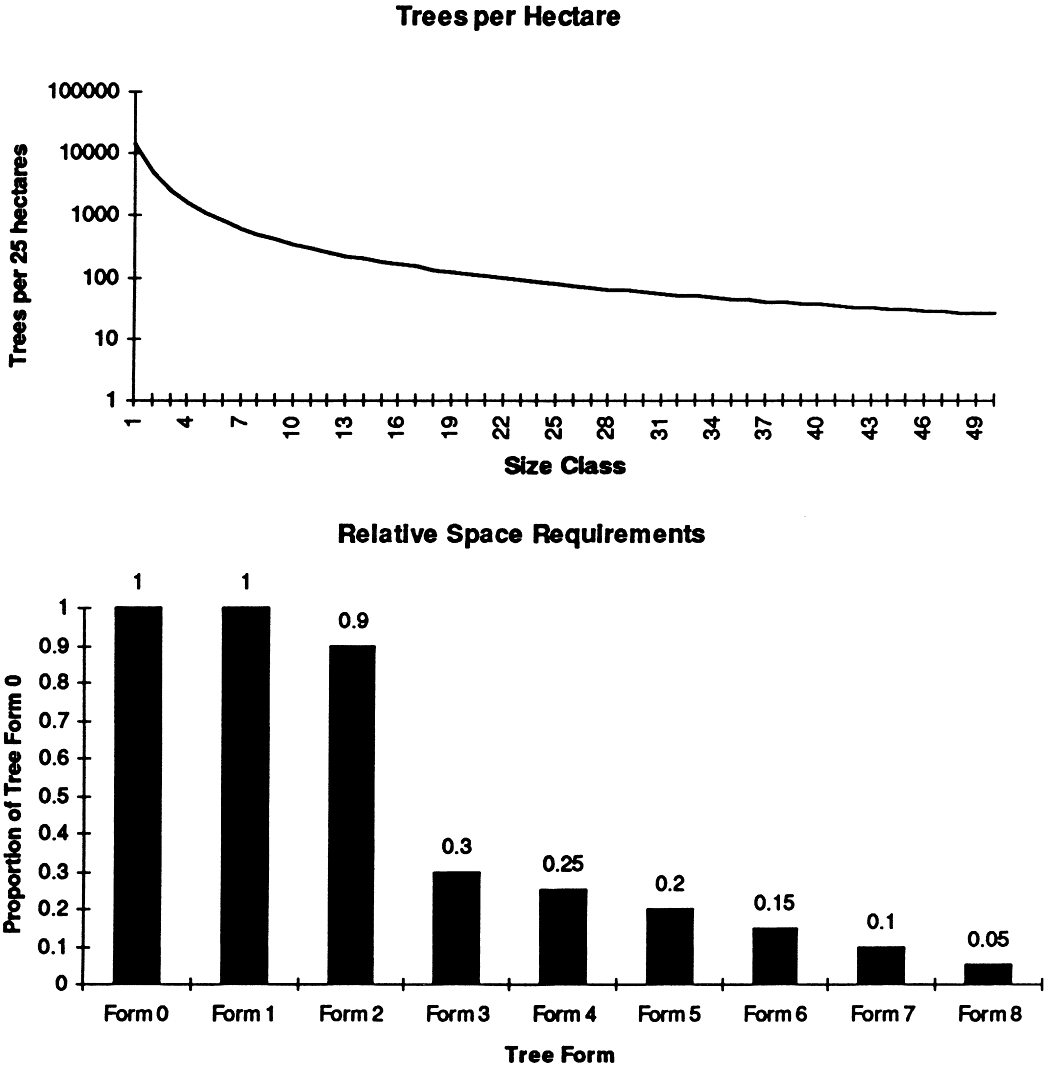

Fig. 5. Spatial requirements: (a) maximum number of Form 0 trees ha^{-1} (calculated from Ashton, 1976), and (b) the amount of space used or required by trees of different forms. These are given as a proportion of the amount of space a tree of Form 0 uses.

the impacts of wildfires have been excluded. During the recruitment phase, trees fill out the first size class (trees <5 cm) so that the forest is again at maximum stocking.

2.7. Timber harvesting

Timber harvesting is managed through the harvesting sub-model, which allows the user to simulate most of the typical harvesting regimes used in Australian forests. There are two types of harvesting. In the first type, the user specifies the number of trees of a particular quality to be retained. An example might be to retain five 'good' trees and three 'mediocre' ones on every hectare, where the characteristics of 'good' and 'mediocre' trees are specified in the sub-model. For example, 'good' could be all trees between size classes 26 and 50 (the maximum size class) which are in tree forms 0 or 1 and 'mediocre' could be defined as trees in tree forms 0, 1 and 2 (i.e. living stems) and between size classes 16 and 18. The second type of instruction is the removal of a proportion of trees in any given state or range of states. A simple example of this prescription is to remove 100% of trees below a certain size which have no hollows. A number of harvesting instructions can be combined to make a harvesting operation and any number of different harvesting operations can be included in a rotation period. The operations in a rotation period are repeated for the length of the simulation.

The model does not allow any distinction to be made between the trees in any single state. Hence, if one tree is retained in a particular state, it will be an average tree and cannot be a tree which is exceptional in any characteristic for that state. Harvested trees are completely removed from the system and no count is kept of them.

When trees are set aside for retention and the rest of a stand is harvested, there is an increased rate of mortality for those retained stems. This higher mortality rate is caused both, by the increased exposure of the trees to changed wind, temperature, and other environmental features after logging and the effects of high-intensity post-logging burns used to promote regeneration. Mortality rates can be set in the programme as the proportion of the retained trees which will collapse within a single time step. The default setting for this is zero, which means that there is no additional mortality or accelerated rates of collapse for retained trees. The results of field observations (Lindenmayer et al., unpublished data) indicates that we would expect 50% or more of retained trees to collapse soon after logging.

2.8. Hollows

The dynamics of three types of hollows in trees can be followed in this model. This is especially important for fauna species that prefer specific hollow types. These types of hollows, for mountain ash trees, are holes, fissures, and hollow branches. For each tree form and size class, there is an expected number of each of these hollows per tree. This can be used to calculate the expected number of each type of hollow for the entire stand. The values for mountain ash are displayed in Fig. 6 and they are based on extensive statistical analysis by Lindenmayer et al. (1993). The default output of the model is the number of trees which have hollows, rather than the total number of different types of hollows summed across all hollow-bearing stems of given types within the stand. The programme also has the option of allowing the examination of each of the different types of hollows individually.

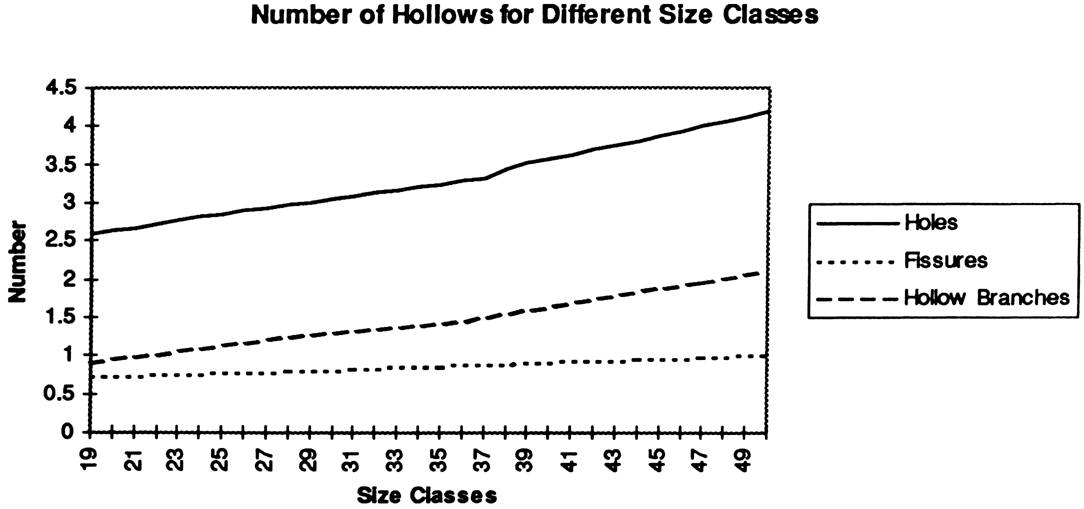

Fig. 6. Number of different types of hollows in Form 1 trees (living with hollows) of different size classes. Adapted from Lindenmayer et al. (1993).

2.9. Output

HOLSIM allows the user to specify two types of output. It can produce a time series of the number of hollow-bearing trees in the stand, or the number of a particular type of cavity (i.e. a hole, hollow branch or fissure). Additionally, it can extract the minimum, average, and maximum number of hollow-bearing trees over a pre-defined period. For the scenarios described below, we extracted the 'steady-state' statistics on the hollow dynamics by setting the statistical extraction period to 650–749 years. This was ample time for each of the scenarios to achieve a stable cycle of number of trees with hollows and predicts hollow dynamics if a harvesting system is implemented over a long time.

The minimum number of hollow-bearing trees was the primary measure taken in our study. This was because it is a reflection of the likelihood that a stand would support trees suitable for occupation by hollow-dependent animals (Gibbons and Lindenmayer, 1996).

2.10. Scenarios explored

We simulated three harvesting strategies in this study. In each of them, a specified number of trees are retained and the rest removed during each harvesting event. In every scenario, we use a 25-ha logging area and a fixed rotation time. In the first set of simulations, only trees which already contained hollows were retained. In the second set of simulations, the quota of trees to be retained was met by first retaining trees with hollows, and then the other trees if necessary. In both these sets of simulations, there was no extra mortality of the retained trees associated with each harvesting event. The number of trees retained per hectare was varied along with the harvest rotation length between each simulation. In the last set of simulations, retained trees suffered higher post-harvest mortality due to the effects of increased exposure and also a high-intensity regeneration burn following logging. Here, we explored the impact of changing the rotation time and increased harvest-related mortality levels on hollow dynamics. In all scenarios, the forest started as a newly cleared stand with a 150-year period before the next tree harvesting event.

3. Results

3.1. Scenario 1: Retention of hollow bearing trees

To ensure the stand supported some trees with hollows at any particular time, it was first harvested, and logging did not begin until 200 years after initial disturbance. In each scenario, 10 trees ha^{-1} were retained at every tree harvest, the rest being removed. Only trees which already had hollows (tree forms 1–8) were eligible for retention (when there are <10 trees ha^{-1} with hollows on the stand, then all are retained). The effect of the rotation length on the hollow dynamics was explored with rotation lengths of 50, 100, 120 and 150 years.

The number of hollow-bearing trees peaks before the first logging event and then tends towards zero (Fig. 7). The strategy fails to sustain hollows in the long term, because 50 years is too short for hollows to develop. The only hollow-bearing trees that remain in the system are those left after the first cycle. When the rotation time is 100 years or longer, it is possible for new trees with hollows to develop and numbers eventually reach a non-zero equilibrium (Table 3). This equilibrium usually occurred after 1000 year, and is well below the 10 trees ha^{-1} which we might naively expect.

3.2. Scenario 2: Retention of trees with or without hollows

In this scenario, when there were not enough trees with hollows to fill the retention quota, other trees were retained to make up the numbers, starting with the largest stems. As in Scenario 1, there was no added mortality among retained trees following harvesting.

Table 3
The long-term number of trees with hollows which arise when up to 10 trees with hollows per hectare are retained with varying rotation times

Retain only trees with hollows	
rotation length	trees with hollows per ha
50	0.00
100	0.44
120	1.80
150	2.81

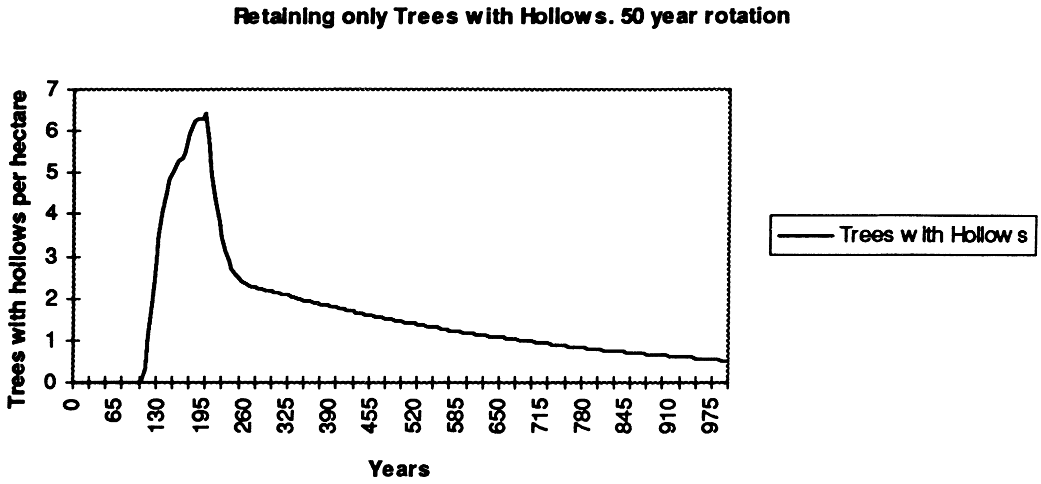

Fig. 7. A time series showing a logging regime where, at each harvest, up to 10 trees with hollows are retained in each hectare and the rest are removed. The stand starts as a newly cleared stand and the first harvest occurs in Year 200. The harvest rotation is 50 years.

This might correspond to a situation where effective windbreaks are added to protect retained trees, perhaps clumping all the retained trees across the 25-ha stand, and where logging debris was dispersed without burning. Rotation lengths of 50 and 100 years were tested with the number of trees retained per hectare being 1, 5, 10, and 20. The performance measure is the minimum number of trees which had hollows between the years 650 and 749. This length of time was chosen to allow the system to settle into a cycle. Generally, the system had stabilised much sooner than 650 years. The harvesting event occurred at the end of the cycle and the stand was allowed to grow for 50 years before the cycle started.

Fig. 8 displays the results of one run in Scenario 2. The minimum values that occur when the system stabilises is given in Fig. 8(b). The graph shows the increasing number of trees with hollows supported at different levels of tree retention. Our simulations suggest that the harvest rotation time has little effect on the abundance of hollow-bearing trees when there is no extra post-logging mortality.

3.3. *Scenario 3: Tree retention with post-logging mortality – 10 trees ha^{-1} retained*

The final scenario examined focussed on the effects of mortality of trees that were retained after timber harvesting. Rotation lengths of 50 and 100 years were tested. The level of mortality of retained trees immediately after a harvest was varied between 0% and 90%. The output was the minimum number of hollow-bearing trees which occurred between 650 and 750 years.

The results from this series of simulations are displayed in Fig. 9 and they show that the minimum number of hollow-bearing trees tapers off quickly as mortality increases. This decline is more dramatic when the rotation time is 50 rather than 100 years.

4. Discussion

4.1. *Retaining trees with hollows*

It is quite clear from our simulations that a harvesting strategy only retaining trees which already have hollows is a disastrous method for ensuring that a given level of trees with hollows is maintained. Mountain ash trees only start to form hollows after a minimum of 90 years (Ambrose, 1982); and, if all of the trees without hollows were removed each 50 years, new ones would never form (Fig. 7). With a rotation time of 100 years, the number of trees with hollows remains small. This situation can be ameliorated by increasing the rotation time or by retaining recruit trees which have not yet formed hollows, but which will eventually form hollows (Scenario 2).

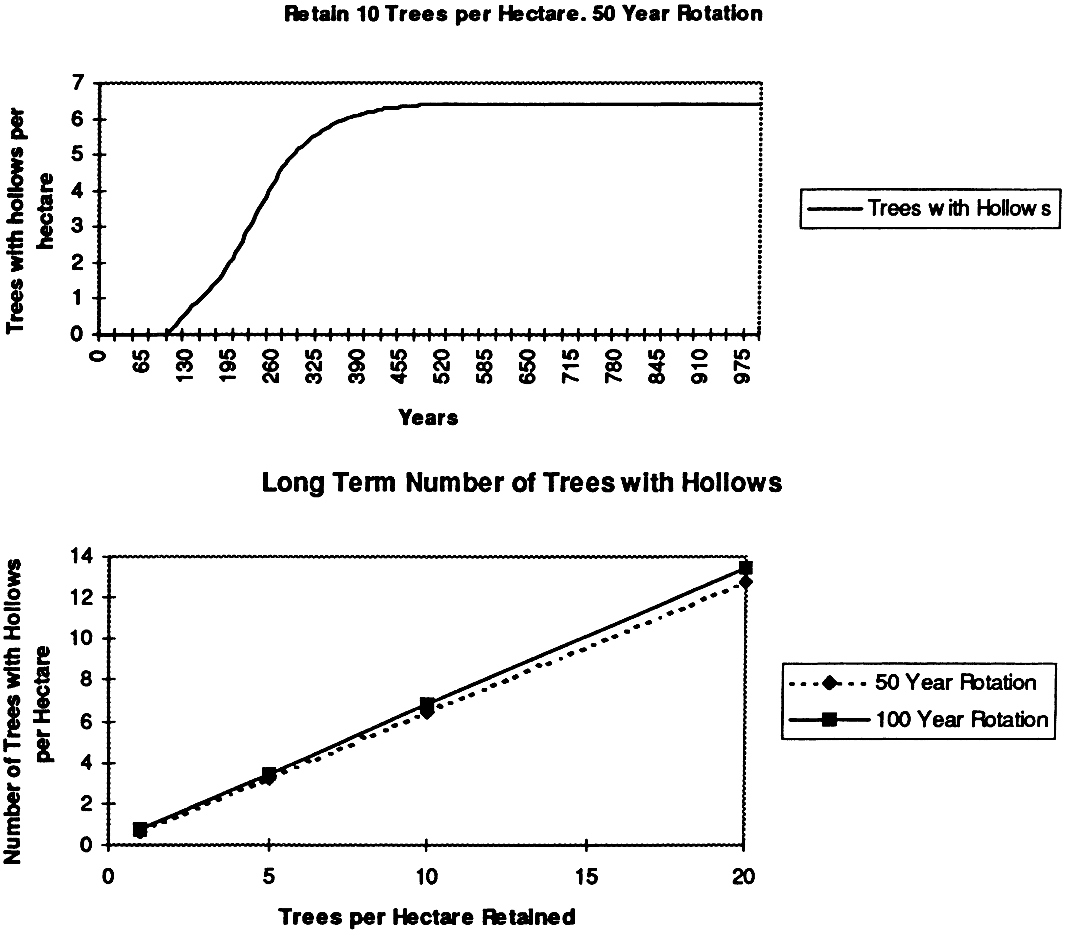

Fig. 8. Results from Scenario 2. (a) Time series from a single run. The logging regime has 10 trees ha^{-1} retained (with or without hollows) and a 50-year rotation. The first harvest occurs at 200 years. (b) The minimum number of trees with hollows per hectare in each rotation cycle after the simulation has stabilised. It is plotted against the number of trees retained.

In the second scenario, a set number of trees are retained whether or not they all have hollows. For a rotation length of 100 years or less, if only one tree per hectare is set aside – but this tree need not have hollows (Fig. 8), we still end up with more trees having hollows than the case where we can retain up to ten trees per hectare, but only those which are already hollow-bearing (Table 3). As the rotation times increase, there is less discrepancy because more trees form hollows between harvests.

4.2. Tree retention without post-logging mortality

When there is no post-logging mortality, the number of trees which have hollows is directly proportional to the number of trees per hectare being retained. This proportion is relatively stable with varying numbers of trees retained and under different harvesting intervals. Approximately 35% of the trees being retained are not hollow-bearing stems, but they will replace the existing hollow-bearing trees that are lost as a result of mortality.

4.3. Tree retention with post-logging mortality

It was not surprising that the number of trees with hollows decreases as the mortality rate increases. The interesting result is that this change is not linear. For example, when there was 50% post-logging mortality, the number of hollow-bearing trees remaining was less

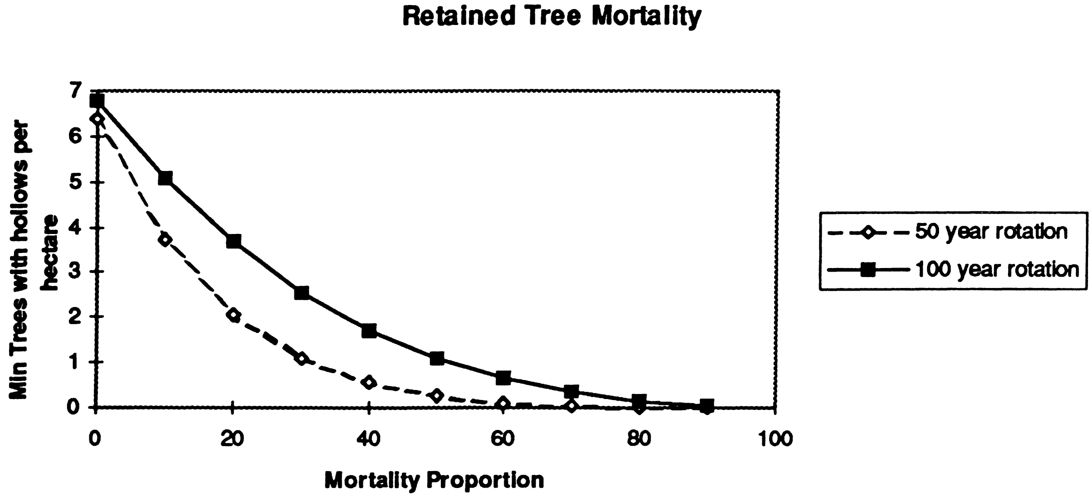

Fig. 9. Results from Scenario 3. The minimum number of trees with hollows per hectare which occur in a rotation cycle after a steady cycle has been reached. Mortality proportion is the proportion of trees which are to be retained, but collapse immediately following a tree-harvesting event.

than half the number which occurred when there was no additional post-logging mortality. This is evident when a 100-year rotation was implemented, and it is much stronger when the rotation length is only 50 years. The reason that this occurred is that with each cut, a proportion of all retained trees collapsed (notably the largest stems which were being preferentially retained). When there was limited mortality, these trees persisted through several harvesting events and fewer of the retained trees need be small hollowless trees. However, with added mortality, few trees may grow large enough for hollows to form. Replacement is limited because of the length of time it takes for a tree to form hollows.

4.4. Assumptions and limitations

The main limitations of HOLSIM were that:

- the stand consisted of a single species of trees;
- every year was the same, with no year-to-year environmental variability;
- there was no spatial complexity in the stand; and
- random catastrophes, like fire, were not considered.

The primary limitation of the model is that the modelled stand consists of a single species of trees. This is appropriate in the study because stands of mountain ash are generally dominated by this one species. The effects of other organisms on the system are assumed to be constant or insignificant, and presumably limited to non-tree species (such as shrubs and insects). While many harvested stands have several tree species, if the hollow-forming properties are similar, then this model may still be useful to explore the impact of various logging and tree-retention strategies.

Spatial complexity is not included in the model. If complete information of the position of every tree and the geography of every hectare were included, then it would be difficult to parameterise the model and would add no further insight into the impact of different management options. More detailed spatial information might be useful for a stand which contains gross geographic features, such as half of it being on a steep slope and the other half on flat ground. However, in this case, the model could be used by simulating the two sub-stands independently and then combining the results.

Catastrophes were not included in the model. Random events could not be added to the model without turning it into a Monte-Carlo simulation, which would then require extensive repetition to generate results. Fires are an important part of Australian forest ecology and excluding them places some constraints on the applicability of the model. However, as the model represents an average forest, the inclusion of fires would be very difficult. Wildfires can have a substantial effect on an individual stand, but they occur at unpredictable time intervals. It is, however, possible to study the effects of a particular fire event at a specific time. If one were interested in observing the effects of a single fire on a stand, then the fire could be simply included as a special type of timber harvesting operation.

5. Conclusions

HOLSIM is intended to be a planning tool for wildlife planners and forest managers to help them forecast long-term stand conditions arising from forest management regimes. The programme aids in the examination of the potential effects of an array of interacting factors that influence the dynamics and structure of forest ecosystems. It can be used to determine whether given management strategies are likely to meet particular stand-structure targets that have been set by managers. It also allows managers to anticipate the possible impacts of forestry operations on hollow-dependent fauna.

There are a number of points which arose from the mountain ash scenarios which have implications for tree harvesting operations upon these forests. These are presented in the following.

- It is clear that it is not sufficient to retain only those trees which already have hollows unless a very long (>100 years) rotation cycle is in place. As the hollow-bearing trees age and collapse, it is necessary to retain trees which are not yet hollow bearing in order to replace them with those that are.
- When the retained trees are *completely* protected from the normal factors which increase mortality during, and following a harvesting event, and retained trees are not restricted to those already possessing hollows, the minimum number of trees with hollows is independent of the rotation length. In this case, the number of trees with hollows which persist on the stand is simply proportional to the number which are retained.
- Additional mortality associated with logging on retained trees cannot be countered simply by reserving more trees so that the same number survive. This is because of the non-linear effect of the additional mortality. For example, when there is 50% mortality of retained trees, it is not enough to double the number of trees retained to get the same number of trees with hollows persisting in the stand. A greater proportion of the trees retained must be ‘recruitment’ trees, which do not yet have hollows, but are being retained to replace those which do as they age, collapse, and suffer tree harvesting-related mortality.
- A short rotation time can greatly exaggerate the effect of additional post-logging mortality. This implies that introducing measures to reduce post-logging mortality could well be the most cost-effective way of ensuring the persistence of adequate numbers of trees with hollows. Such measures could include the retention of trees in clumps to decrease effects of exposure and clearing brush from the base of retained trees before applying post-logging regeneration burns.

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