Modelling the spread of wilding conifers [*]

Industry representatives: Philip Grove and Yvonnne Buckley
Problem moderators: Mick Roberts and Heather North

March 16, 2005

Abstract

In many parts of the Canterbury high country conifer seeds are spreading on the wind from exisiting plantations and shelterbelts, leading to a serious weed problem. Environment Canterbury set the task at MISG to model this spread, and thus establish a basis for prioritising control operations on a limited budget. The study group provided increased

---

[*] Report arising from the Mathematics in Industry Study Group held at the University of Auckland, 26–30 January 2004. Contributors: Boris Baeumer (University of Otago), Alona Ben-Tal (University of Auckland), Bronwyn Bradshaw-Hajek (University of Wollongong), Yvonne Buckley (Imperial College, London), John Butcher (University of Auckland), Bruce Calvert (University of Auckland), Paul Dellar (OCIAM, Oxford, UK), Amanda Elvin (Massey University), Philip Grove (Environment Canterbury), John Kean (AgResearch), John King (University of Nottingham), Darren Kriticos (Forest Research), Carlo Laing (Massey University), Shona Lamoureaux (AgResearch), Leng Leng Lim (Massey University), Joanne Mann (Massey University), John Moore (Forest Research), Mark Nelson (University of Wollongong), Heather North (Landcare Research), Mick Roberts (Massey University), Tim Svenson (University of Sydney), Ngamta Thomwattana (University of Wollongong), Yi-Jing Tsai (University of Auckland), Bruce van Brunt (Massey University). MISG participants would also like to acknowledge valuable input from Nick Ledgard, Forest Research.

understanding of topographic and climatic factors involved in seed dispersal, and of the distribution of the resulting seed rain. In addition, a simulation framework was developed for comparing the effectiveness of different control strategies.

1 Introduction

As a regional council, Environment Canterbury is responsible for many aspects of environmental protection and sustainability. A major weed problem has been recognised in the form of wilding conifers spreading from existing plantations and shelterbelts. These threaten native vegetation and important wildlife habitat, as well as impacting on pastoral farmland and the visual and recreational values of Canterbury landscapes. A recent survey by Environment Canterbury mapped over 60 thousand hectares of conifers, including both plantations and wildings. They estimated that wind dispersal of seed from these sources threatens a further one million hectares of land. Under the Regional Pest Management Strategy (2002) Environment Canterbury has some funding for wilding conifer control, but this is limited relative to the scale of the problem. Thus, the control budget needs to be strategically allocated to achieve the best possible environmental outcomes for the dollars spent. The problem posed to the MISG centred on modelling wilding conifer spread, with the overall aim of prioritising sites for control operations.

The study group focused on three interrelated aspects. The first was to develop an understanding of the topographic and climatic drivers of seed dispersal, the second to model dispersal once the seed has been released, and the third to analyse and model management options. The industry representatives provided practical field knowledge and a detailed dataset of wilding tree locations (distance and orientation from original seed source) for invasive *Pinus nigra* (Corsican pine) at Mount Barker near Lake Coleridge, Canterbury. The study was motivated by the existing collaboration between new Zealand and the United Kingdom (Buckley et al. 2004). We report here on work at the Maths in Industry Study Group held in January 2004 as well as subsequent work carried out by individuals from the study group.

2 The mechanisms of seed dispersal

In order to identify which exisiting conifer sites pose the greatest risk to the surrounding land, it is important to understand the topographic and climatic drivers of short- and long-distance seed dispersal. Fringe spread occurs when seed is released from a tree and is carried some horizontal distance by the wind, until it falls to the ground under the force of gravity (Figure 1). If the maximum release height is h, and the seed quickly reaches some terminal velocity v_{term} under the force of gravity, then with an average windspeed of $\bar{u}$, a simple model for maximum dispersal distance is:

$$d = \frac{h\bar{u}}{v_{\text{term}}} \tag{1}$$

Data from the Mount Barker site was used to estimate possible fringe spread distance. *Pinus nigra* cones mature during late autumn to early winter (May–July). Warm, low humidity conditions encourage cones to open [N. Ledgard, Forest Research, pers. comm.]. These conditions are provided by the predominant north to north-west winds that are channelled down Lake Coleridge and over Mount Barker. Seed can drop from the cones soon after opening, but if a strong wind occurs at this time, the seed can be carried further from the

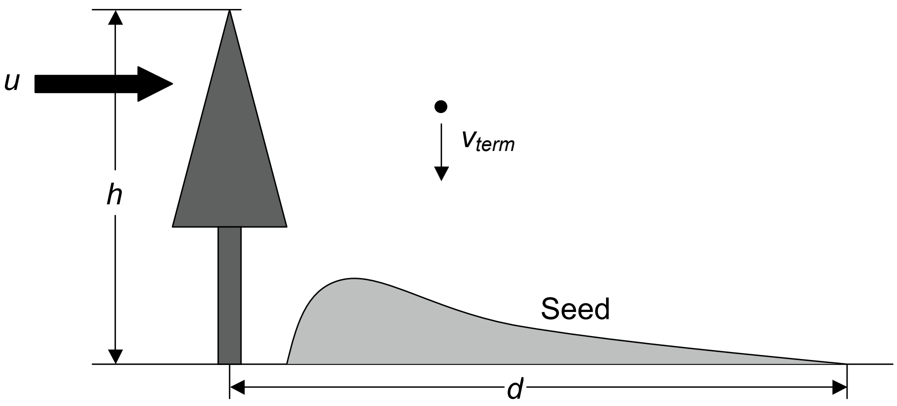


Figure 1: Fringe spread, where seed falls from maximum release height, h, reaching some terminal velocity, v_{term} under the force of gravity. Seeds travel a maximum distance, d, for an average windspeed of $\bar{u}$.

tree. We analysed windspeed data from the nearby Snowdon weather station, obtained via the NIWA climate database, for the months May to July in 2000 to 2003.

Table 1 shows windspeed data from June 2003 for each speed and direction category, expressed as a percentage of observations for the month. These are average hourly windspeeds, but note that maximum gust speeds within each hour are significantly higher, ranging up to 28 m/s (100 km/h). We have selected a typical windspeed of $\bar{u} = 8$ m/s for calcuation of fringe spread distances. This is the average windspeed from the north and north-west directions during June, and there is seldom a period of more than 4 days without wind of this speed or more. Thus a proportion of the seed has a high probablility of being carried downwind rather than falling directly to the ground. In Eq. 1 we used $v_{\text{term}} = 0.8$ m/s [N. Ledgard, Forest Research, pers. comm.; Greene and Johnson (1995)] and $h = 10$ m, giving an estimate of about 100 m for fringe spread. This estimate is in agreement with field observations of the industry representatives.

Hourly av. windspeed	N	NE	E	SE	S	SW	W	NW	All dir.	Spread from 10-m tree
0–6 m/s	19	11	3	0	9	2	0	7	51	0–75 m
6–14 m/s	17	0	0	0	0	0	0	28	45	75–175 m
>14 m/s	1	0	0	0	0	0	0	4	4	>175 m
All speeds	37	11	3	0	9	2	0	38	100	

Table 1: Occurrence of windspeed/direction categories at Mount Barker, June 2003, expressed as a percentage of total observations for the month. Note that, on average, the maximum gust speed in an hour is more than twice the hourly average windspeed.

Fringe spread is mostly clearly seen at Mount Barker as teardrop-shaped tails of young pines downwind from isolated mature trees in current aerial photography. Greene and Johnson (1995) also note the “sink” effect in the lee of a forest stand where windspeeds are low, so that seeds are quickly deposited from the airstream. This effect causes gradual downwind expansion of a dense forest stand, or infilling of a sparse stand.

The tail of wilding *Pinus nigra* now extends almost 10 km down-valley (downwind) from the original seed source, which was situated to the north-west of

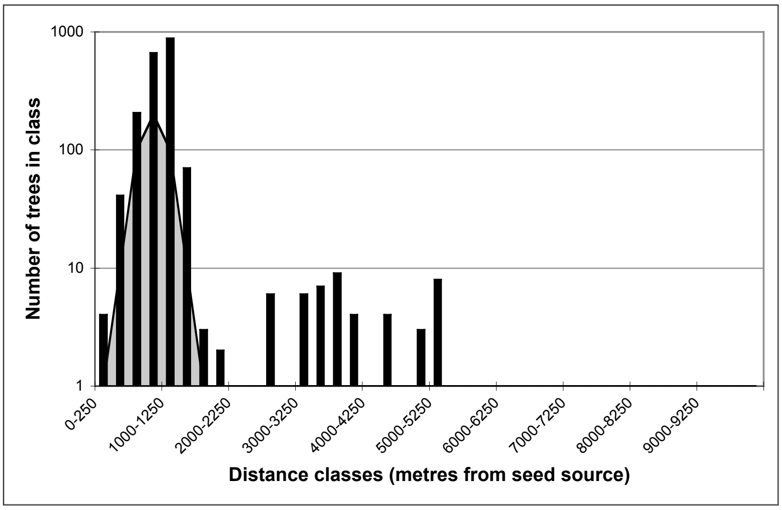
Mount Barker (though this source has since been removed). Figure 2 shows tree distributions in 1965 and in 1980, derived from aerial photography. The source trees were planted in approximately 1910, and probably started coning about 15 to 20 years later.

The distributions of Figure 2 are clearly not explained by fringe spread. Fringe spread would cause the invasion front to advance only about 100 m in each 15- to 20-year generation, a distance of only 400–500 m in the 70 years from 1910 to 1980. Industry representatives were aware that mature trees were distributed throughout the tail, and that their age suggested infrequent long-distance dispersal events rather than gradual spread. The trees in the 1965 diagram would have had to be at least 10 years old at that time to be visible in the aerial photograph, suggesting a dispersal event prior to 1955.

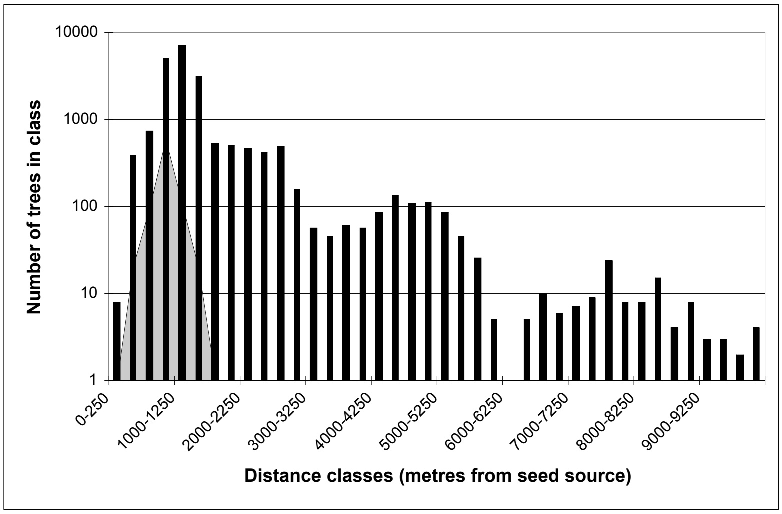
Observations from a field trip subsequent to MISG2004 confirmed that there had probably been three further major dispersal events. Trees of age approximately 20, 30 and 45 years were seen in the tail (7.5 km from the source), suggesting discrete dispersal events in approximately 1960, 1975 and 1985. The distribution of these trees suggested that each age group had arisen from a separate long-distance dispersal event, rather than the younger (20 and 30 year old) trees arising by fringe spread from the older (45 year old) trees.

Two questions are raised by these observations: the first concerns the mechanisms by which seeds can travel as far as 10 km from their source; and the second is why these events occur so rarely—perhaps every 15 years or so.

To achieve the long dispersal distances observed in invasive field situations, the group showed that the effective release height of the seeds had to be much greater than tree height. Tackenberg (2003) suggests thermal uplift as an important mechanism for this height gain. However, this seemed unlikely at the



(a) 1965



(b) 1980

Figure 2: Distributions of *Pinus nigra* at Mt Barker, Canterbury, as a function of distance from the original seed source; (a) in 1965 and (b) in 1980. The approximate location of Mount Barker is shown as the grey polygon.

Mount Barker site. Strong north-west winds are the norm when the temperature is high, so thermal uplift is probably rare. Tackenberg (2003) and Greene and Johnson (1995) discuss vertical turbulence set up by windy conditions as a mechansim for uplift, and the latter use this as the basis of their long-distance-dispersal model. Tackenberg, however, argued that mechanical updrafts from stormy weather are usually too brief to raise seeds to the observed height, and that downdrafts dominate over updrafts.

Tackenberg also briefly discussed the role of topography in seed uplift. The MISG group thought that Mount Barker itself was functioning as a launching ramp for seeds released from the mature trees upwind of the hill. The seeds could be carried by the wind up and over to be effectively released at a height at least 270 m above the surrounding land. Even though the great majority of seeds would be dropped in the area of low pressure in the lee of the hill, some would continue on the airflow.

To achieve the 5.5 km tail observed in 1965 (just over 4.5 km from the effective release point at the top of Mt Barker), and working from Eq. 1 with $v_{\text{term}} = 0.8$ m/s and $h = 270$ m, a horizontal windspeed of $\bar{u} = 13$ m/s (50 km/h) would be needed. For the 10 km tail in 1980 (just over 9 km from release point), $\bar{u} = 27$ m/s (95 km/h) would be needed. Even from just one year's data (Table 1), it appears that windspeeds of this magnitude do occur. Note also that the windspeeds in Table 1 are surface winds, and speeds at 270 m elevation are likely to be greater.

Why then are these long-distance spread events so rare—for example, only three to four major events at Mount Barker in 70 years—if topographic uplift can occur so easily? One possibility is that the dispersal events do in fact happen frequently but germination and seedling establishment is poor, so that we see a cohort of trees surviving only infrequently. *Pinus nigra* cones only every 2–3 years, and it is possible that some years are too droughty for successful seedling establishment. However, seed remains viable for approximately 3 years, so can wait for suitable conditions. Grazing intensities vary throughout the area, but little is managed so intensively as to kill off all young trees. Most of the area is unimproved tussock grassland where seedling establishment success is between 20% and 90% depending on grazing intensity [N. Ledgard, Forest Research, pers.comm.]. Thus poor germination or seedling establishment is unlikely to be the reason for the discrete age classes.

The reason is more likely related to the chances of very strong wind occurring during the short period of time when seeds are ready to detach (before they fall out of the cones of their own accord). From the 2000–2003 NIWA climate data, there are usually several days during each June when average hourly wind speeds reach 16–20 m/s. However the 27 m/s speed estimated (above) for a 9-km spread event is less common. It does not occur at all as an average hourly wind speed during the 4-year period for which we have data, though there are typically two occurrences each June where maximum gust speed (in an hour) reaches 25–30 m/s. Maximum gust speeds of this magnitude are even less common in July (when cones open in some environments) and a single gust may not be sufficient for dispersal in any case.

All the conifers in the main long-distance dispersal tail from Mt Barker appear to have arrived there in one of the four discrete events described above (excluding more recent fringe spread around these mature trees). It is understandable that strong winds capable of carrying seeds 9 km may be relatively infrequent, but it is less understandable that there would not be many events of intermediate speeds leading to intermediate dispersal distances. Some initial calculations at MISG showed that wind at slower speeds would tend to go round, rather than over, the hill, so seeds may not obtain the required release height. These initial calculations suggested that a windspeed of some 13 m/s may be required for the airflow to ramp up and over the top of Mount Barker. There is some evidence to suggest that the wilding *Pinus nigra* to the south-west of Mount Barker (1 km from the original seed source) do indeed have a more continuous age distribution [N. Ledgard, Forest Research, pers. comm.] so lower wind speeds carrying seed around the western flanks of Mount Barker may be a possibility. Further work is needed in this area.

3 Modelling seed dispersal

The second area of effort at the MISG was modelling the dispersal of seed once it has been released. There are several distributions suggested in the literature for modelling the density of seed rain and the distances travelled. These models describe the high seed densities that fall out of the airstream close to the source, and the long tail of seed that travels the greater distances. It is the outermost edge of the tail that determines the invasion speed of the conifers. Thus it is important to correctly model the distance and seed rain density for those seeds which travel the farthest, in order to correctly predict invasion speed. For example, Neubert and Caswell (2000) modelled the spread of trees via a non-linear integral equation

$$n_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y) b\left(n_t(y)\right) n_t(y)\,\mathrm{d}y$$

Here, $n_t(y)$ is the population density at time t and location y, b is the population birth rate, which depends on local density, and k is a dispersal kernel which is a function only of the distance $|x-y|$. This model implies an outward spread with wavespeed

$$c^* = \min_{s>0} \frac{1}{s} \log \left(b(0) \int_{-\infty}^{\infty} k(x) e^{sx} \, \mathrm{d}x \right)$$

Okubo and Levin (1989) modelled airborne seed dispersal from a single source. Defining $S(x, y, z, t)$ to be the concentration of seeds at position (x, y, z) and time t, with x downwind, y the orthogonal horizontal direction, and z vertically upwards, the diffusion model is

$$\frac{\partial S}{\partial t} + u(z) \frac{\partial S}{\partial x} - v_{\text{term}} \frac{\partial S}{\partial z} = \frac{\partial}{\partial z} \left(D(z) \frac{\partial S}{\partial z} \right)$$

The wind velocity profile is written

$$u(z) = (\alpha + 1) \, \bar{u} \left(\frac{z}{h} \right)^{\alpha}$$

for some constant α, and the diffusion coefficient profile

$$D(z) = 2\bar{D} \frac{z}{h}$$

The boundary conditions at $z = 0$ are

$$D(z) \frac{\partial S}{\partial z} + (v_{\text{term}} - v_d) \, S = 0$$

where v_d is the deposition velocity of seeds at the ground; and $S \to 0$ as $|x|$, $|y|$, $z \to \infty$. Hence the probability distribution of seeds at ground level is

$$k(x) = \begin{cases} A x^{-B} \exp\left(-\frac{C}{x}\right) & : \quad x > 0 \\ 0 & : \quad \text{otherwise} \end{cases}$$

with $B = 1 + v_{\text{term}}/v^*$ and $C = h\bar{u}/v^*$. Okubo and Levin (1989) provide a survey of values of v^*/v_{term}, the ratio of vertical mixing velocity to terminal velocity. This ratio is small for heavy seeds, and large for pollen. The distribution $k(x)$ is plotted in Figure 3 for two species of pine.

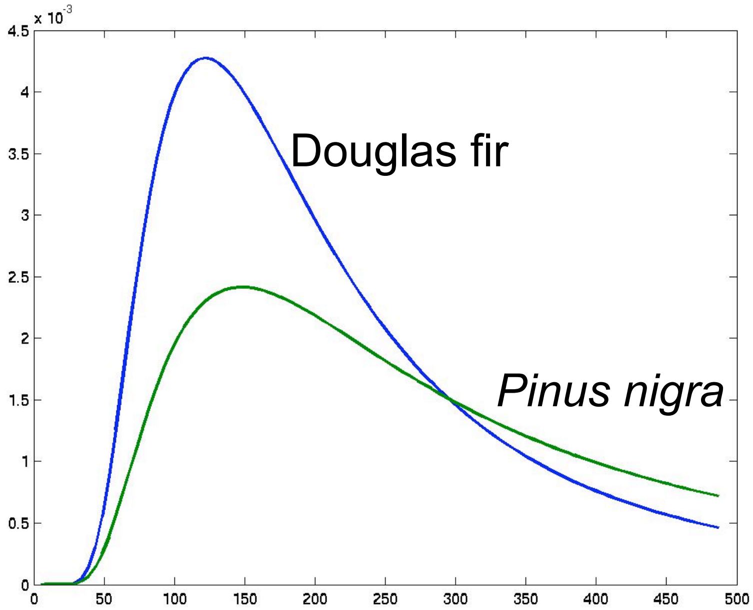


Figure 3: Probability distribution of seeds of two pine species at ground level, as a function of distance (in metres) from the source.

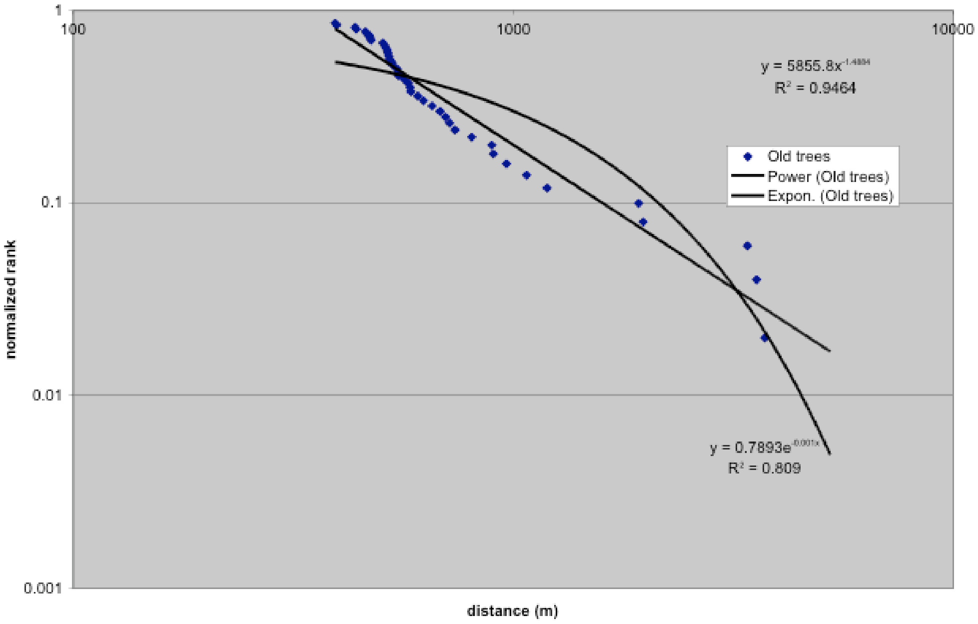


Figure 4: Data from Mount Barker, showing the normalised distribution of mature trees on a log scale, compared with the fitted power law (straight line on a log scale) and exponential curves.

For large values of x the distribution $k(x)$ may be approximated by a power law. In Figure 4 data from Mount Barker is plotted on a log scale, and compared with fitted power law and exponential curves. Although the curve $y = 5855x^{-1.5}$ appears to be an excellent fit, this would imply $v^*/v_{\text{term}} \simeq 2$, which would be more appropriate for lighter seeds than those of *Pinus nigra* (see Table 1 in Okubo and Levin, 1989). Hence, while the Okubo and Levin model gives a tantalizingly close description of the data in many ways, the data are closer to model predictions that would be relevant for lighter seeds; and of course the model is based on an assumption of steady rather than intermittent dispersal. It would be interesting to see if the data are consistent with the superimposition of a few short-term dispersal events using this model.

4 Management options for wilding conifers

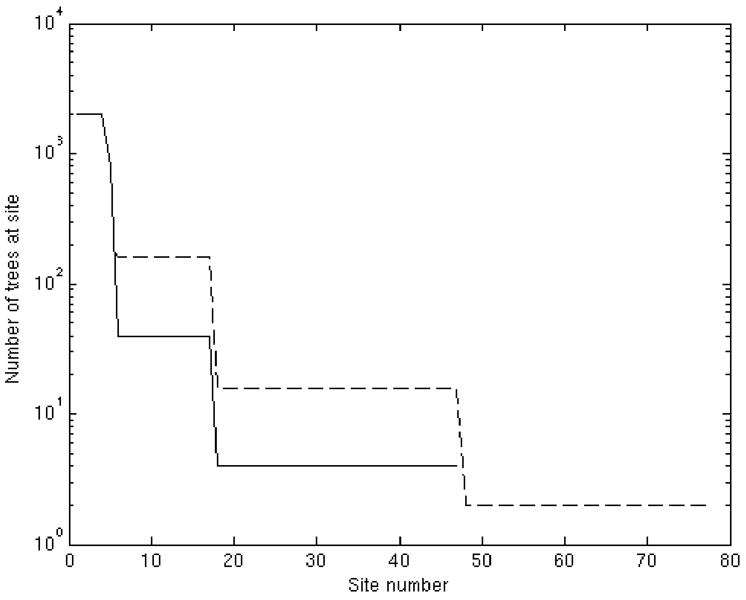
There is a range of management options for controlling conifer spread, each more or less effective in different situations. In some cases, wilding conifers are growing in a small, dense patch, perhaps arising from fringe spread around a mature shelterbelt. It is often possible to eradicate the entire patch. In other cases long-distance spread may have occurred from source trees, leading to a large area of sparse trees. It is not always economically possible to remove all of them in any given year, and deciding how to approach the control problem is more complex. Depending on factors such as tree age, budget and other resources available, and the natural significance of the downwind landscape, one may choose to remove some or all of the mature source trees, or some or all of the dispersed wildings.

To address this, we first developed pragmatic models of invasion as a series of discrete steps occurring in a downwind direction. One approach was to define a set of possible transitions from young to old and scattered to dense trees, and assign probabilities to these. This enabled a computer simulation of year-on-year invasion to be developed. A second approach modelled invasion as a cellular automata. Each year seedlings were added to downwind cells (in one dimension), according to rules for number of seedlings produced annually by a mature tree, and how many of these will remain local and how many will disperse further. This model, too, was written as a simulation and iterated to model year-on-year invasion.

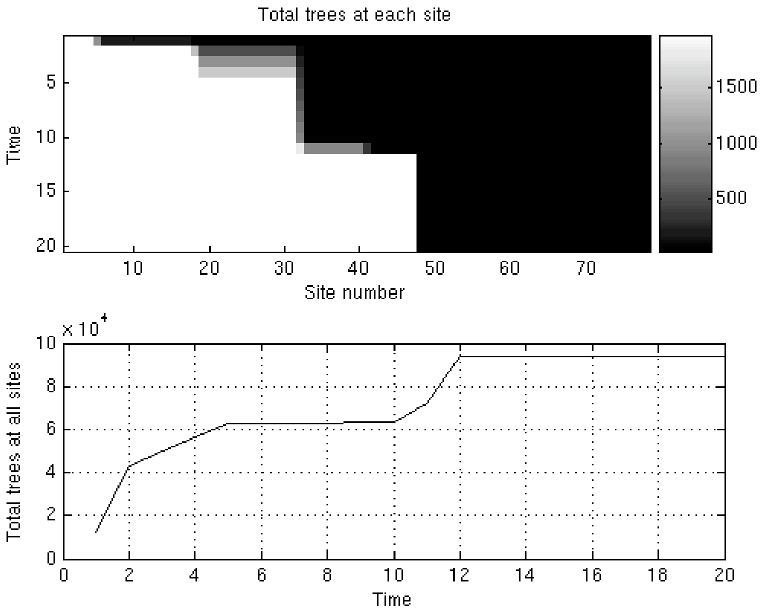
Into this model of spread were added control operations. Knowing that there was not sufficient budget to remove all trees in a single year, the task was to find the management strategy that provided the best control of the invaded area. A range of possible management strategies was defined, such as always targeting the largest patches of trees for removal, or always targeting the oldest. In each year of the simulation, the number of new trees at each site was calculated, and a number of trees were removed according to the chosen management strategy.

Early simulations at MISG indicated that targeting the youngest trees (equating to the outermost edges of the tail of wilding conifers) was more successful that targeting the mature (coning) trees. However, subsequent investigation of assumptions behind the spread model brought improved realism. While initially each site containing mature trees had been assumed to produce a constant number of seedlings, the subsequent model produced seedlings in proportion to the number of mature trees at a site. In this model the mature trees exercise greater influence on the the number of seedlings dispersed and it is generally more successful to control the oldest trees. The reality is probably somewhere between these two models, with seedling production initially increasing with the number of mature trees, but quickly becoming constant once the mature canopies close and seed is produced mainly from the sunlit edges of the stand rather than the centre. Figure 5 shows output from the most recent version of the spread/control model operated for fringe spread only. This demonstrates better control when mature trees are removed each year than when young trees are targeted, even though in the model it is assumed that it is more expensive to control mature trees, and thus fewer can be removed each year.

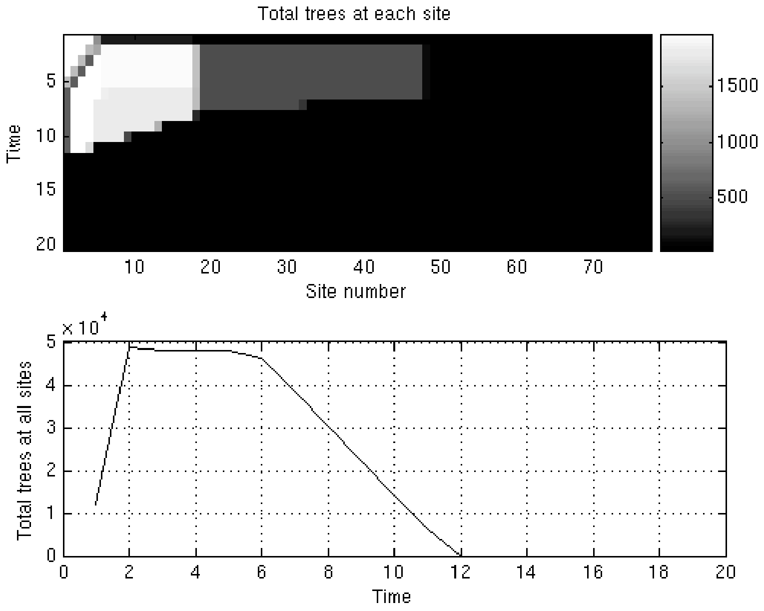
Work on this topic is ongoing, to improve the realism of the spread model and to introduce dollar-value costs for each of the control strategies. This simulation has the potential to provide a valuable framework for predicting and visualising the effect of various control strategies.



(a)


Total trees at each site
Time
5
10
15
20
10
20
30
40
50
60
70
Site number
1500
1000
500
× 10^4
Total trees at all sites
10
8
6
4
2
0
0
2
4
6
8
10
12
14
16
18
20
Time

(b)


Total trees at each site
Time
5
10
15
20
10
20
30
40
50
60
70
Site number
1500
1000
500
× 10^4
Total trees at all sites
5
4
3
2
1
0
0
2
4
6
8
10
12
14
16
18
20
Time

(c)

Figure 5: An example of the cellular automata spread/control model, (a) number of trees in each 1-ha site for initialising the model, totalling 9400 mature trees (solid line) and 2660 younger trees (broken line), (b) control strategy removing youngest trees first, then progressively older trees, (c) control strategy removing oldest trees first then progressively younger trees. Parameters: annual budget available for removing 2000 mature trees (can remove four immature trees for the same cost as one mature tree), trees become mature after 15 years and thereafter cone every 3 years, producing 100 new seedlings in the local site and 25 in the next/downwind site, i.e., simulating fringe spread only.

As well as prioritising within a site, a limited budget requires that control operations are prioritised between sites. It is necessary to consider three issues: (1) the extent of the area threatened by potential seed rain from existing mature trees—which requires an understanding of wind, topographic uplift and the shape of the dispersal kernel, as discussed in this report; (2) the vulnerability to establishment and the natural significance of the area threatened by such seed rain; and (3) the budget available and level of site access.

5 Conclusions

The group at the MISG has increased understanding of topographic and climatic drivers of wilding conifer dispersal distances and event frequency. A more realistic model of seed rain density has been tested, supporting more accurate prediction of invasion speed. These developments are important for site risk assessment. A framework has been developed for modelling conifer invasion in space and time, and for predicting the level of control expected from various management strategies.

References

Buckley, Y.M.; Brockerhoff, E.; Langer, L.; Ledgard, N.; North, H.; Rees, M. 2004: Slowing down a pine invasion despite uncertainty in demography and dispersal. Submitted to Ecological Applications.

Greene, D. F. & Johnson, E. A. 1995 Long-distance wind dispersal of tree seeds. Canadian Journal of Botany 73, 1036-1045.

Neubert, M. G. & Caswell, H. 2000 Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81, 1613-1628.

Okubo, A. & Levin, S. A. 1989 A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecology 70, 329-338.

Tackenberg, O. 2003 Modelling long-distance dispersal of plant dispores by wind. Ecological Monographs 73, 173-189.