

The impacts of possum herbivory and possum control on threatened palatable species (*Pittosporum patulum*, *Alepis flavida* and *Peraxilla tetrapetala*) in the Lake Ohau Catchment, South Island, New Zealand

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Abstract

The impacts of possum herbivory were assessed on 713 individual plants of the nationally endangered *Pittosporum patulum* and 115 individual plants of the threatened ('Gradual Decline') mistletoes (*Alepis flavida* & *Peraxilla tetrapetala*) over three years in the Temple and Huxley river valleys in the Ohau catchment, South Island New Zealand. Statistical models were used to test the influence of several explanatory variables on the probability of survival and growth rates of these rare palatable plants. Increasing defoliation levels were the most significant predictors of mortality for both *P. patulum* and mistletoe, and reduced growth rates in *P. patulum*. Mortality of *P. patulum* increased with plant size although smaller plants were also affected by mortality. *P. patulum* mortality was greater for non-forest habitats, and growth rates were greatest on warm aspects. Mistletoe mortality increased with warm aspect, steeper slopes and at lower altitudes. Plant survival and growth increased in the Temple valley following possum control. Although indicative of a positive treatment effect, other factors may have also influenced this result. Possums are the major herbivore responsible for the widespread decline of *P. patulum* and beech forest mistletoes throughout New Zealand, although the autecology of *P. patulum* predisposes it toward extinction more so than mistletoe. Monitoring in conjunction with possum control operations provide good opportunities for understanding the impacts of possums on palatable plants and ecosystems. Assessing defoliation levels on indicator species like *P. patulum* and mistletoes can serve as a guide for managers to assess ecosystem stress from herbivory.

Contents

Abstract	i
Contents	ii
List of figures	iv
List of tables	iv
1. Introduction	1
Study species	6
Objectives	10
2. Methods	12
The study area – Temple and Huxley river valleys	12
Data collection <i>P. patulum</i>	15
Data collection mistletoe	17
Assessing defoliation	18
Monitoring	19
Possum control operation	19
Data analysis <i>P. patulum</i>	20
Defoliation index	22
Site variables	23
Probability of survival	23
Growth rate	23
Data analysis mistletoe	24
Probability of survival	24
3. Results	26
Pre-poison comparisons (2002)	26
Age class composition of <i>P. patulum</i>	26
Defoliation levels	26
Changes in defoliation levels between 2002 and 2004	27
Treatment area (Temple catchment)	27
Non-treatment area (Huxley catchment)	28
Age-dependent defoliation effects	31

Changes in mistletoe foliage cover	32
<i>P. patulum</i> survival	33
Relative growth rates of <i>P. patulum</i>	36
Mistletoe survival	38
4. Discussion	40
Impact of herbivory	40
Environmental influences	43
Catchment effect	46
Patterns of defoliation and long term trends	49
Long term sustainability – extinction!	50
Conservation implications	52
Review of monitoring	55
5. Conclusions and recommendations	58
6. References	61
Acknowledgments	68
7. Appendix one	69
Standard recording sheet	69

List of figures

Figure 1	<i>P. patulum</i> age classes	9
Figure 2	Adult <i>P. patulum</i> in sub-alpine shrubland	9
Figure 3	Heavily defoliated <i>P. patulum</i>	9
Figure 4	Map of study area	13
Figure 5	Defoliation levels of <i>P. patulum</i> 2002-2004	29
Figure 6	Defoliation levels of mistletoe 2002-2004	30
Figure 7	Defoliation levels of adult <i>P. patulum</i> 2002-2004	32
Figure 8	Probability of survival plotted against defoliation for <i>P. patulum</i> age classes	35
Figure 9	Relationship between relative growth rates of <i>P. patulum</i> and defoliation levels	37
Figure 10	Probability of survival for mistletoe plotted against defoliation	39

List of tables

Table 1	Proportions of <i>P. patulum</i> plants in each age class in the treatment and non-treatment areas	26
Table 2	Percentage of dead <i>P. patulum</i> plants in each age class in the treatment and non-treatment areas in 2004	31
Table 3	General Linear Models showing probability of <i>P. patulum</i> survival	33
Table 4	Change in relative growth of <i>P. patulum</i> between 2002 and 2004	36
Table 5	General Linear Models showing probability of mistletoe survival	38

1. Introduction

Herbivory from the introduced brushtail possum (*Trichosurus vulpecula*) on native forest and shrubland communities is a significant ongoing threat to New Zealand's indigenous biodiversity. Of particular concern is selective heavy browsing of a few preferred palatable species. The resulting prolonged possum herbivory can change forest composition, alter successional pathways, and in extreme cases may induce complete forest collapse (Coleman *et al* 1985; Atkinson 1992; Rose *et al* 1993; Parkes 1994, Owen and Norton 1994; Bellingham *et al* 1999; Pekelharing and Batchelor 1990, 1998; Rogers 1995, 1997; Rogers and Leathwick 1997; Payton *et al* 1997; Norton 2000; Nugent *et al* 2000; Nugent 2002). While individual species may be dramatically affected, corresponding impacts on ecosystem health may be of more serious concern to New Zealand's conservation efforts. For example, competition by possums on native fruit resources may have adverse impacts on many native avian species. Consequences of this competition may include a reduction in many bird species' fecundity (Leathwick *et al* 1983, O'Donnell and Dilks 1986; Owen and Norton 1994; Cowan and Waddington 1999, Sweetapple *et al* 2004).

A further concern to conservation is the effect possum herbivory has on many palatable rare species and the threat this poses to their survival (Crawley 1983; Dopson *et al* 1999, de Lange 1998; de Lange *et al* 1999; Rogers and Walker 2002; Hitchmough 2002). This may be most significant when rare palatable species occur in floristically simple, low diversity ecosystems because possum herbivory has a disproportionately greater impact on forest composition and long-term ecosystem health (Owen and Norton 1994). This is highlighted by analyses of possum stomach contents taken from low diversity beech forest in south Westland. In their study, Owen and Norton (1994) found uncommon

palatable species make up a disproportionate amount of food in the stomach contents of possums, compared to common species.

Despite the impacts of possum herbivory on ecosystem health and functioning being well documented, the actual threat that possum herbivory poses to the long term survival of many palatable and rare species remains to be clarified (Stewart and Veblen 1982; Bellingham *et al* 1999; Allen *et al* 2002). Although 62% of threatened species are considered nationally threatened with extinction due to mammalian herbivory, including possum browse (Dopson *et al* 1999), this is primarily based on anecdotal field observations. In reality, there is limited quantifiable evidence to support claims that possum herbivory will eventually lead to plant species extinction.

New Zealand's beech forest mistletoe (*Peraxilla tetrapetala*, *P. colensoi*, *Alepis flavida*) are examples of this. These mistletoe species have declined markedly throughout their natural range. This decline is largely attributed to possum herbivory (Rance and Rance 1996; Sawyer 1997; Dopson *et al* 1999; Sessions 1999; Sessions *et al* 2001). However debate exists over the actual threat possums pose to mistletoe due to 'negligible' possum impacts occurring at some sites despite continued long term possum presence (Wilson 1984; Owen and Norton 1994; Ladley and Kelly 1996; Ladley *et al* 1997; Sessions and Kelly 2001a, 2001b).

Several studies have attempted to clarify the impacts of possum herbivory on mistletoe species, and have evaluated control methods to protect mistletoe populations. Protection methods include collaring trees, poison and trapping (Rance and Rance 1996; Ladley and Kelly 1996; Sessions *et al* 2001). Although these studies consistently highlight a relationship between possum presence and degradation of mistletoe plants, the precise impact that possums have on mistletoe remains unclear (Owen and Norton 1994; Ladley and Kelly 1996; Sessions and Kelly 2001a, 2001b). However, highly significant responses of mistletoe

to possum control in some specific areas means mistletoes are often used as forest health indicators to judge the success of possum control operations. For example, mistletoe health and presence is used as a general measure of ecosystem health in the Department of Conservation (DoC) Hurunui Mainland Island (Sessions *et al* 2001; Sweetapple *et al* 2002).

Other than mistletoe, few studies that have investigated the long term possum impacts on the sustainability of palatable rare species in low diversity plant communities. While there are numerous anecdotal reports of local losses of palatable plant species resulting from possum herbivory, there has not been a record of a native plant species becoming nationally extinct from possum herbivory.

Extinction requires an imbalance between recruitment and mortality (Crawley 1983; Bellingham *et al* 1999; Dopson *et al* 1999), resulting over time in population decline to a point from where recovery cannot occur. The potential for extinction depends on various physiological and ecological traits of a species that influence its vulnerability to a potential threat, such as herbivory. Generally the risk of extinction is higher for species that occur in small isolated populations or have low habitat plasticity (Lesica 1992; Gaston 1994; de Lange and Norton 1998; de Lange *et al* 1999; Duncan and Young 2000; Hitchmough *et al* 2002; Rogers and Walker 2002).

Quantifying the risk of extinction caused by possum herbivory is difficult due to the complexity of interactions between ecosystem processes and possum herbivory (Stewart and Veblen 1982; Nugent and Sweetapple 1997; Pekelharing *et al* 1998; Allen *et al* 2002). Typically impacts from possum herbivory are regionally inconsistent between similar ecosystems, and as a result, any wide ranging generalisations about possum impacts beyond specific sites need to be treated with caution (Green 1984; Owen and Norton 1994; Allen *et al* 2002)

These inconsistencies are partly due to different species responding differently to possum herbivory, which may be a consequence of diverse life history traits and autecologies. For example, tree fuchsia (*Fuchsia excorticata*) and wineberry (*Aristotelia serrata*) are highly palatable 'seral' species that seem able to persist in relative abundance despite prolonged heavy herbivory by possums (Allen *et al* 2002). These species are relatively short lived and deciduous species. Consequently these are able to refoliate rapidly after leaf loss. Conversely cedar (*Libocedrus bidwillii*) has limited ability to recover from heavy herbivory events and will die following up to 75% defoliation regardless of no further herbivory (Rogers 1997; Rogers and Leathwick 1997; Allen *et al* 2002).

Compounding the above is the highly selective and seasonal nature of possum herbivory (Coleman *et al* 1985; Rogers and Leathwick 1997; Pekelharing *et al* 1998; Owen and Norton 1994; Allen *et al* 2002). Typically this involves some plants being heavily defoliated and others being left alone. Often plants are heavily defoliated, then may be ignored by possums for long periods while the foliage recovers at which point they will be revisited. This temporal variation in herbivory may be the result of micro site differences (soil, aspect etc) making some plants more palatable than others. For example, one study found there to be more death from possum herbivory of palatable species on fertile soils than on soils of poor fertility, which were considered to be more preferable possum habitat (Rief and Allen 1988).

The presence of other mammalian herbivores makes determining the impact of possums difficult. This is especially pronounced in the lower tiers of ecosystems where several herbivore species are present and compete for the same resources. In particular red deer (*Cervus elaphus scoticus*), chamois (*Rupicapra rupicapra*, Himalayan tahr (*Hemitragus jemlahicus*), hares (*Lepus europaeus*), rats (*Rattus* spp), and many invertebrate species feed on understory species (Belovsky 1986; Parkes 1994; Hobbs 1996; Forsyth *et al* 2000). Separating the impacts of possums from these other herbivores in the lower forest tiers has proven

difficult. Consequently, many studies attempting to determine species and herbivore browse patterns have produced mixed results (Nugent *et al* 1997; Sweetapple and Burns 2002; Wilson *et al* 2003). Accordingly, much of our understanding of possum impacts comes from research on forest canopies, as generally the foliage is out of reach from most other herbivores. However, analyses of possum diet shows that ground foraging makes up a major proportion of possum diet at certain times of year (Coleman *et al* 1985; Owen and Norton 1994; Rogers 1997; Nugent *et al* 2000). Therefore understanding the impact of ground foraging is important to determine the impact of possum feeding on plant recruitment success (i.e. seedling establishment) and the ability of an ecosystem to maintain 'normal' species composition and ecosystem function over long periods of time (Crawley 1983).

Our ability to understand the impacts of possum herbivory on the long term survival of species depends on robust long-term monitoring and data collection methods that best describe a herbivore impact (Allen *et al* 2002). Unfortunately most monitoring programmes have been established long after possum incursion. Limited data on vegetation composition prior to possum presence creates difficulties in establishing a cause and effect relationship due to secondary and lag effects associated with a history of herbivory. This is compounded a majority of programmes, being short term, and cannot capture long term trends or account for existing impacts (Allen *et al* 2002).

In the absence of data from possum free ecosystems of interest, removing possums from an area and monitoring the response traits of selected palatable species over time is one option available to assess possum impacts. In addition, sophisticated statistical models are relatively new techniques that allow numerous biological inferences to be made from complex ecological data (Burnham and Anderson 2001; Johnson and Omland 2004). These powerful statistical tools can provide new insights and understanding of ecosystem interactions.

Study species

Pittosporum patulum is a highly palatable small tree species of beech forests and adjoining sub-alpine communities along the eastern South Island of New Zealand. It is distributed sporadically from North West Nelson to the head of Lake Hawea in Central Otago, although there is an unexplained distribution gap in mid Canterbury in the Rangitata river catchment (Rogers and Walker 2005).

The habitat in which *P. patulum* occurs is commonly the mid to upper headwater valley systems of steep greywacke mountains. It is usually under mountain beech (*Nothofagus solandri* var *cliffortioides*) forest in light gaps associated with ridgelines and bluffs, sub-alpine shrublands near the tree line and at the head of valleys where beech has failed to colonise, disturbed areas associated with snow and rock avalanche, and riparian margins of tributary streams. It is also known to occur under silver and red beech (*N. menziesii*, *N. fusca*) in a few sites but this situation is atypical (van Eyndhoven and Norton 1999; Roger and Walker in press). *P. patulum* displays traits typical of other seral species. It shows relatively rapid growth, and is reliant on disturbance and 'stable' light gaps under forest canopies to provide sites for the recruitment and maintenance of sexually mature populations (van Eyndhoven and Norton 1999; Rogers and Walker 2005).

P. patulum goes through distinctive growth phases and associated morphological changes; from seedling, sapling, sub-adult to adult (Figure 1). This is a feature of numerous New Zealand tree species (Eagle 1982; Townsend 1999). The seedling and sapling stages are typified by a slender pole stage, which is sparsely vegetated with narrow toothed leaves. The adult stage is a stout tree up to 6 meters tall, and can be the dominant emergent tree species in shrubland communities (Figure 2). Adults have a dense leafy crown with short, thick entire leaves (Townsend 1999).

P. patulum appears to be going through a prolonged phase of population decay and decline throughout its natural range. This has largely been attributed to browsing by introduced herbivores (Dopson *et al* 1999; van Eyndhoven and Norton 1999; Rogers and Walker 2005). In particular, possums have been implicated in the death of adult trees, and are the only introduced herbivore capable of reaching the adult crowns of *P. patulum* (Figure 3). Herbivory on seedlings and saplings in lower tiers is attributed to a variety of ground dwelling mammalian herbivores, such as hares, deer, goats, rats and insects (as well as possums) (Rogers and Walker 2005).

Selective heavy browsing of adult *P. patulum* by possums is thought to occur because they are a locally abundant and preferred food resource in generally resource-poor ecosystems. In addition, an adult plant can support the weight of a possum in its crown. This makes adult plants an energetically more efficient food resource compared to seedlings and saplings, which being sparsely foliated, are a less obvious and nutritionally less valuable resource (Nugent *et al* 2000; Brian Molloy pers. com.). Consequently, it is thought that possum herbivory has skewed the population structure of *P. patulum* toward younger sapling and seedling plants as adults specimens are targeted and killed by repeated heavy defoliation events. This has induced an inverse J population distribution (van Eyndhoven and Norton 1999; Rogers and Walker 2005). The resilience of adults (and other age classes) to browsing, and the ability of plants to recover from herbivory is unknown.

Although the loss of adult *P. patulum* has been attributed to possum herbivory, and in particular the length of possum occupation (Cowan 1990; Clout and Ericksen 2000; Nugent *et al* 2000, Roger and Walker in press), other than inference from herbarium records and field observation, there is no historical demographic data to use as a comparison with modern data to judge trends (Rogers and Walker 2005). Until recently, very little quantifiable research had been undertaken to specifically investigate this decline.

Despite a lack of quantifiable evidence, *P. patulum* is listed as a nationally endangered species by DoC (Hitchmough 2002), resulting in a Recovery Plan for the species (Townsend 1999). Because of this high threat rank, DoC undertook a survey of all known (historical) records of *P. patulum* during the summers of 1999 and 2000 in an attempt to understand more about its conservation status. This survey confirmed the absence of adults throughout the entire species range. However, the lake Ohau catchment was an exception (in particular the Temple and Huxley river valleys). Here the only populations of *P. patulum* that contained significant numbers of adult trees were found (Head 1998).

This survey confirmed that the Temple and Huxley valleys contain the most intact populations of *P. patulum*, and that these closely resemble its historical composition (Head 1998; Rogers and Walker 2005). At these sites, possums are considered a recent incursion and are at pre-peak possum densities, whereas they have had a long presence in areas where *P. patulum* was considered more abundant than it is today (Cowan 1990; Clout and Ericksen 2000). This may explain why there is a relative abundance of adult *P. patulum* and mistletoe in the area today (Rogers and Walker 2005).

Peraxilla tetrapetala and *Alepis flavida* are two highly palatable loranthaceous mistletoe species parasitic of beech forests communities found throughout New Zealand. Both species are relatively host-specific, primarily occurring on southern beech (*Nothofagus*) trees, where they can grow up to several meters in size (Norton 1997; Sessions and Kelly 2001b). The habitat where these mistletoe species occur is widespread throughout New Zealand (Norton 1997). In the study area, these mistletoes occur throughout on mountain beech forest, although they appear to be more abundant in the lower valleys.

Like *P. patulum*, the brushtail possum has been blamed for the decline of native mistletoe species (Ogle and Wilson, 1985; Sessions *et al* 2001; Sessions and Kelly 2001b). Studies on mistletoe recovery after possum



Figure 1. Age classes of *P. patulum* from left to right: seedling, sapling, sub-adult, adult (photo G. Rogers).



Figure 2. Adult *P. patulum* in sub-alpine shrubland, Huxley valley (photo M. Beardsley).



Figure 3. Heavily defoliated adult *P. patulum* (photo J. Barkla).

poison operations show that mistletoe can be a reliable indicator of possum impacts (Sessions and Kelly 2001b). In addition, there is also anecdotal evidence which suggests that some correlation exists between the duration of possum presence and the decline of mistletoe populations (Ogle and Wilson 1985; Brockie 1992; Ogle 1997). Both *A. flavida* and *P. tetrapetala* are listed as nationally threatened species ('Gradual decline') by DoC (Hitchmough 2002). In addition, DoC has prepared a Recovery Plan for New Zealand's loranthaceous mistletoe species (Dopson 2001).

In 2002 DoC undertook a possum control operation in the Temple valley to protect *P. patulum* and mistletoe, and established a monitoring project to assess changes to these species in the treatment area. Equivalent monitoring was established in the Huxley valley to assess responses in *P. patulum* without possum control, and to allow comparisons to be made between treatment and non-treatment areas. Mistletoe was included in the monitoring project in an attempt to determine if this species is a key indicator of possum damage as described by previous studies (Rance and Rance 1996; Sessions *et al* 2001).

Objectives

The objective of this project was to assess the impacts of possum defoliation on *P. patulum* and mistletoe in the Temple and Huxley valleys of the Lake Ohau catchment. If *P. patulum* and mistletoe were being degraded and killed by possum defoliation in the Temple and Huxley valleys, a response in the condition of these species should have occurred following the removal of possums (assuming they were reduced to sufficiently low numbers) relative to the non-treatment area where possums remain.

Specifically, the objectives of this study were to follows:

- Provide a pre-poison overview of possum impacts on *P. patulum* and mistletoe in the treatment and non-treatment areas
- Describe the patterns of defoliation on *P. patulum* and mistletoe in the Temple and Huxley between 2002 and 2004
- Assess the relationship between defoliation and environmental conditions on the probability of survival and relative growth rates of *P. patulum*
- Assess the relationship between defoliation levels and environmental conditions on foliage cover and probability of survival of mistletoe.
- Provide an assessment of conservation implications for these species
- Assess the effectiveness of the current monitoring programme

2. Methods

The study area - Temple and Huxley river valleys

The Temple and Huxley river valleys are steep-sided glacial-shaped valleys that drain to the Hopkins River from the Barrier Range and Main Divide of the Southern Alps, South Island of New Zealand (Figure 4). The Hopkins River is a major tributary to Lake Ohau in the Mackenzie Basin. Both the Temple and the Huxley valleys have a north and south branch, and a main branch, which encompass about 8500 ha and 9500 ha in area, respectively. There is a steep rainfall gradient ranging from 6000mm per annum in the western headwaters to 2000 mm per annum in the eastern lower valley. The underlying parent material is greywacke (Leathwick *et al* 2002).

The vegetation is dominated by mountain beech (*Nothofagus solandri var cliffortioides*) forest which occupies the valley sides to about 1000m. Forest species diversity is low, especially in the lower valleys of both the Temple and the Huxley, presumably due to lower rainfall. The major woody species associated with the beech forests include broadleaf (*Griselinia littoralis*), Hall's totara (*Podocarpus hallii*), *Neomyrtus penduncularis*, *Coprosma* spp, and *Raukaua simplex*, which are usually found along streams and bluffs and are more common in the upper valleys. Silver beech (*Nothofagus menziesii*) is also present in the Huxley valley, especially in the more western north branch.

Extensive sub-alpine shrublands, dominated by turpentine shrub (*Dracophyllum longifolium*), snow totara (*Podocarpus nivalis*) and celery pine (*Phyllocladus alpinus*), occur above the tree line. These shrublands give way to snow tussock grasslands (*Chionochloa rigida*, *C. macra*),

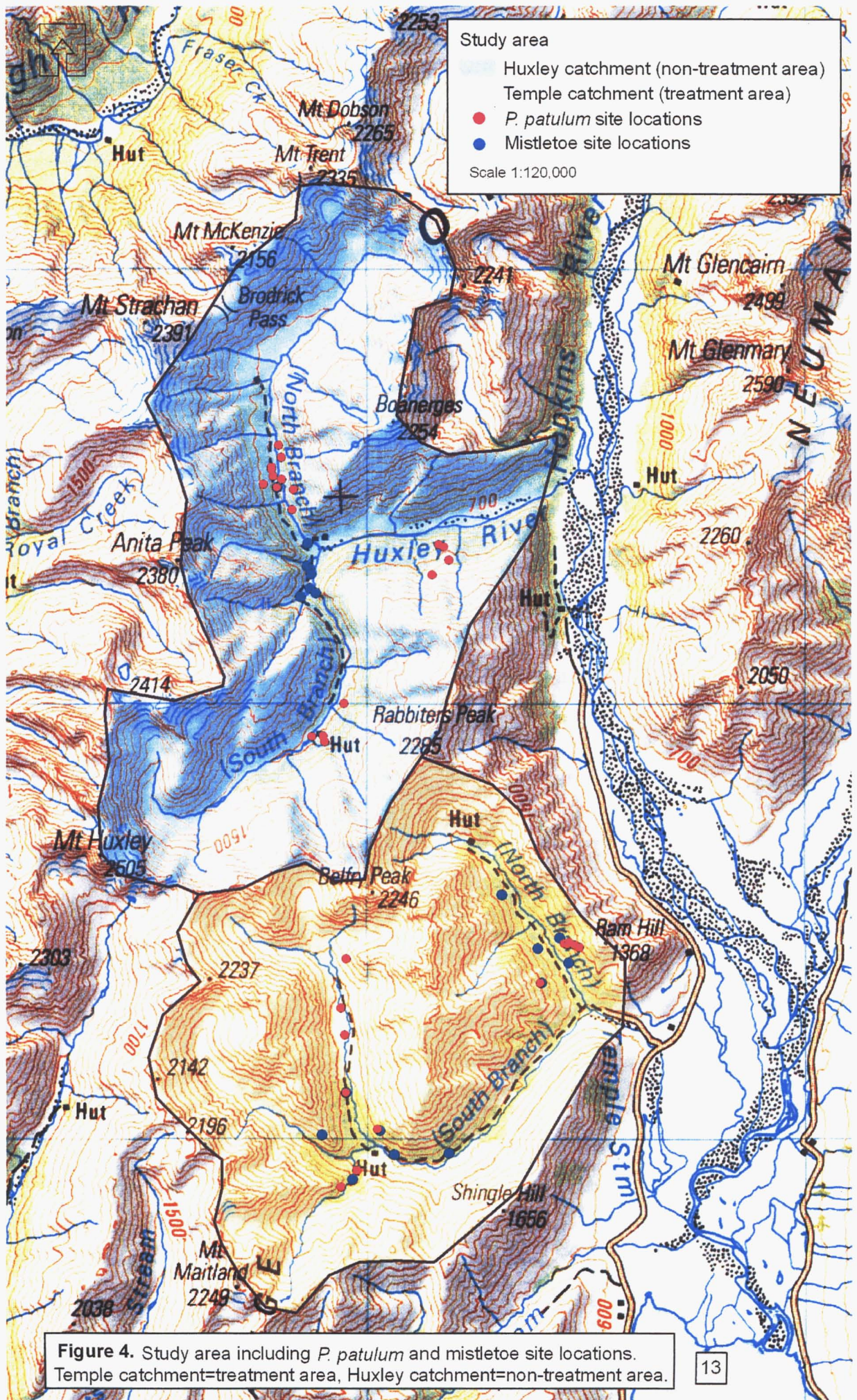


Figure 4. Study area including *P. patulum* and mistletoe site locations. Temple catchment=treatment area, Huxley catchment=non-treatment area.

herbfield and rock (fell field etc) at around 1200 m. Tongues of sub-alpine shrublands as described above, in combination with mainly small-leaved *Coprosma* spp, broadleaf, and sapling mountain beech grow on snow and rock avalanche debris which occurs sporadically on mountain slopes throughout the study area. Mixed shrublands similar to those described above, but including less turpentine shrubs, and abundant bog pine (*Halocarpus bidwillii*) occur at the head of the valleys where mountain beech has been slow to re-colonise following the last glaciation.

The valley floors and outwash fans are dominated by exotic and native grassland, with the exception of the upper valleys where native shrublands occur. These occur in combination with numerous native and exotic herbs.

The lower reaches of the south Temple have had large areas beech forest burnt as part of its pastoral history. These areas have been replaced by regenerating manuka (*Leptospermum scoparium*) and short tussock grasslands that are dominated by hard tussock (*Festuca novaezealandiae*). Exotic grass and herb species make up a significant component of these areas. The remainder of the study area is largely unmodified by pastoralism.

P. patulum is found sporadically throughout the study area, typically in open areas under forest, in sub-alpine shrublands above the tree line, in avalanche-induced shrublands, and in shrublands at the heads of valleys. Mistletoe is present throughout the study area but is especially abundant in the lower valleys where beech forest is dominant. *P. patulum* is absent from the modified areas in the lower south Temple valley.

The Temple valley was chosen as the treatment area due to it containing the best known extant populations of adult *P. patulum* in New Zealand, as well as exceptional populations of mistletoe species (*A. flavida* and *P. tetrapetala*). The Huxley valley was chosen as a comparative non-treatment area due to there being good numbers of both *P. patulum* and

mistletoe present, its environmental similarity and close proximity to the Temple valley. It is considered to be sufficiently well buffered from the effects of possum control in the Temple valley (Cowan 2000).

Data collection *P. patulum*

The Temple and Huxley valleys were thoroughly surveyed for *P. patulum* during March and April 2002 prior to possum control to locate as many plants as possible. Initially this was done by relocating *P. patulum* identified by the New Zealand Forest Service (NZFS) reconnaissance surveys during the 1970s and 1980s (DOC record). Following this, a more extensive survey of likely habitat for *P. patulum* was undertaken throughout the entire Temple and Huxley catchments. Likely habitat included tributary streams, major ridgelines, disturbance-induced shrublands, sub-alpine shrublands adjoining the treeline and shrublands up the heads of valleys.

A helicopter survey of the area was also undertaken. This proved particularly useful for surveying sub-alpine shrublands, as these were the most extensive and inaccessible areas to survey. However, only emergent adult plants were identified by helicopter, as seedlings and saplings were too small to be detected. This resulted in survey bias toward adult plants, especially in the Huxley where two 'adult' sites were discovered.

When plants were found, their location was recorded using a global positioning system (Garmin GPS 12 CX), a site number was assigned, and the surrounding area was searched to locate all plants present. Sites were defined by uniform landscape features representative of the local environment (Allen 1992). In most sites all plants present were measured. On a few occasions, when a very large number of *P. patulum* were found,

a representative sample of the whole site was taken and all plants within the sample were measured.

In total, 18 sites were established in the non-treatment area, and 14 sites were established in the treatment area. A total 713 individual plants of *P. patulum* were tagged and recorded (376 and 337 plants from the Huxley and Temple catchments respectively) (Figure 4).

For each site, a standard recording sheet (Appendix 1) was filled out to collect general information on the site and specific measurements of plants including:

- aspect: classified into eight broad classes (north, east, west, south, ne, se, sw, nw), then combined into either warm (n, nw, w) and cold (e, s, sw, se, ne)
- altitude: approximated from topographical maps (NZMS 260 series)
- habitat type: classified into broad habitat classes: forest (F), forest edge (FE), and shrubland (S)
- slope

Each plant was uniquely identified by attaching a numbered aluminium tag. In addition, a strip of blue or orange PVC flagging tape was tied to each plant to assist with relocation. For each tagged plant the following information was recorded:

- tag number
- height: measured in mm; in some cases where a plant was inaccessible, estimates of height were taken. Plants which have had height estimated were excluded from height change analyses
- diameter: measured in mm at the base of the plant, avoiding obvious nodes or atypical basal swelling
- age class: based on a foliar score using leaf characteristics (1-4): 1=seedling, 2=sapling, 3 sub-adult, 4=adult

- defoliation score: an estimate of the percentage of foliage removed by obvious recent browse (0-3): 0= no browse, 1=1-33%, 2=34-66%, 3=67-100%
- die-back score: an estimate of conspicuous presence of dead branches or branchlets (but not recently defoliated live twigs), recorded as (0-3): 0= no die-back, 1=1-33%, 2=34-66%, 3=67-100%

Data collection mistletoe

Mistletoe monitoring was established in accordance to the best practice for survey and monitoring of Loranthaceous mistletoe (DoC 2002), as follows. Survey for mistletoe plants occurred concurrently with the *P. patulum* survey. When a mistletoe plant was found its location was recorded with a global positioning system (Garmin 12 CX) and a site number assigned. From this initial plant location, a survey of the wider area was undertaken to locate as many plants as possible. The location of each subsequent plant was recorded as a compass bearing and distance (m) from the previous plant, which helped with future relocation of plants. Both *A. flavida* and *P. tetrapetala* occurred in the study area.

Eleven sites were located in the Temple catchment (six in the South Temple, five in the North Temple) and a total of 115 plants were measured (47 in the South Temple and 68 in the North Temple). As only four of these were *A. flavida*, data for both species were combined prior to analysis. Seven sites were located in the Huxley catchment (two in the North Huxley (12 plants) and five in the South Huxley (46 plants). However, mistletoe in the upper Huxley catchment was sparse compared to the lower main valley and only 58 plants were found. Unfortunately time prevented further survey in the lower main Huxley where mistletoes were more abundant.

For each site, a standard recording sheet was filled out to collect general information on the site and specific measurements of the plants including:

- aspect: classified into 8 classified into eight broad classes (north, east, west, south, ne, se, sw, nw), then combined into either warm (n, nw, w) and cold (e, s, sw, se, ne)
- altitude: approximated from topographical maps (NZMS 260 series)
- slope

For each plant found, the host tree was permanently marked with an aluminium tag, a number assigned and the standard recording sheet filled out. In addition, for each plant at each site the following information was collected:

- plant size: three measurements were made (width X 2 (d1, d2) and length) which were combined to give an approximation of overall size
- foliage cover: 0-100%
- die-back: scored as an estimate of the proportion of the total plant: 0= no die-back, 1=light, 2=moderate, 3=heavy, 4=severe, X=unable to estimate.
- defoliation: estimated as the proportion of possum-browsed leaves or severity of possum-related hedging averaged over the whole canopy: (0-5) 0= no browse, 0.5=<5%, 1=5-25%, 2=26-50%, 3=51-75%, 4=76-100%, X=unable to estimate

Assessing defoliation

Lagomorphs and ungulates (hares, deer, chamois and Himalayan tahr), are present in the general area and would also browse *P. patulum* and mistletoe (Parkes 1994; Forsyth *et al* 2000). Lagomorph and ungulate browse would have contributed to defoliation scores, especially on seedling and sapling *P. patulum* plants below 2.5 m in height. Although

symptoms of possum defoliation are quite distinctive (Payton *et al* 1999; Rogers 1997; Rogers and Walker 2005), no attempt was made to separate out defoliation impacts from different mammalian herbivores. Where defoliation was clearly caused by invertebrates it was excluded from the assessment (Sessions and Kelly 2001b).

It was assumed that both the treatment and non-treatment areas contained approximately the same ungulate, lagomorph and invertebrate species in similar densities. Herbivore impacts were considered to be equally distributed between the treatment and non-treatment area. Therefore, any response in the condition of *P. patulum* and mistletoe in the treatment area could be attributed to a possum effect.

Monitoring

Monitoring of *P. patulum* and mistletoe occurred prior to possum control in April 2002. Annual monitoring occurred in 2003 and 2004. To limit seasonal variation and observer bias, monitoring was undertaken at the same time of year and using the same observers.

Possum control operation

The poison operation was designed to reduce possum numbers to the lowest possible level in the Temple valley. Before the poison operation began, residual trap catch (RTC) monitoring was undertaken in accordance with the National Possum Control Association standard procedure (National Possum Control Agency 2000) to determine possum abundance in the treatment and non-treatment area. Average RTC figures were similar at 19.7% and 19.4% respectively. These were considered to be very high densities for beech forest (Andy Grant DoC advisory scientist, pers. com.).

For the poison operation, transects were established along all major ridgelines as these were considered the major possum access routes. Horizontal transects were also established along the forest edge, at the valley floor and along the tree line where possum densities were considered highest (Cowan 2000). Bait bags containing Feratox (cyanide) were stapled to trees approximately every 20 m along each transect. Additional poison was placed in areas considered to be possum 'hot spots'. Pre-feeding with 20 g pellets of Ferrapaste (Connovation Ltd) commenced on the 29th of April 2002. The poison operation commenced on the 6th May and continued until the 30th June 2002.

Post poison RTC monitoring in the treatment area returned figures of 0.8%. Additional monitoring was undertaken six months following the poison operation by randomly selecting a 500 ha block within the treatment area and placing 10 mm wax tags (Connovation Ltd) on the base of trees. Monitoring returned a zero encounter rate. This suggests a very high kill rate with few possum remaining in the treatment area. No additional monitoring was undertaken in the non-treatment area as it was assumed that possum densities remained similar to the original RTC figures of 19.4%

Data Analysis *P. patulum*

Data was entered into an Excel spread sheet in a format suitable for analysis using the statistics program R 1.3.1 (copyright 2001, The R Development Core Team), which was used for all analyses. To avoid pseudo replication, the individual site data for the treatment and non-treatment area were combined and treated as one replicate. The lack of replication limits extrapolation of results beyond the study area.

Simple exploratory analysis was undertaken using graphs and tables to compare defoliation levels between the two catchments. To compare

defoliation levels (0, 1, 2, and 3), mean defoliation scores were plotted for the treatment and non-treatment areas. To explore the change in defoliation levels over time, the proportions of defoliation at each level were compared between years 2002, 2003 and 2004. Defoliation levels were also compared against individual age classes (seedling, sapling, sub-adult and adult) to explore the impact of herbivory on the different age classes.

Differences in defoliation levels as a response to possum browse were not subjected to statistical testing, as we considered survival and growth rates to be more appropriate and reliable indicators of defoliation impacts on *P. patulum* than defoliation levels *per se*. This is because defoliation scores were strongly influenced by previous browse events (Sessions 1999), which are evident on the plant over the years given the generally slow recovery times of plants to possum browse. Furthermore, defoliation scores were more vulnerable to observer bias and also varied with other factors. For instance, defoliation scores can be influenced by herbivory from other sources, such as insect browse (Sessions and Kelly 2001b), and heterogeneity in foliage cover associated with the different age class morphologies.

Accordingly, a series of statistical models were constructed (Anderson *et al* 2001) describing how the probability of survival and growth rates of *P. patulum* changed with the explanatory variables outlined below. For the purposes of this study, these response variables were considered to be the most appropriate and reliable indicators of defoliation impacts on *P. patulum* (Anderson *et al* 2001).

Because data were grouped by site within the treatment and non-treatment area, and hence with-in site measurements were potentially correlated, mixed effects models with site included as a random effect, and explanatory variables included as fixed effects were constructed first. Where the random effect proved to be non-significant, linear models with

only fixed effects were used. The significance of the random effect was determined by comparing AIC values for the random effect model and the GLM model without a random effect, where the model with the lower AIC value was the most parsimonious (Burnham and Anderson 2001). Any plant recorded as dead in 2002 was removed from the data set prior to model fitting.

Defoliation index

A defoliation index was used to estimate the cumulative effect that defoliation has on the probability of plant death, and rate of growth of *P. patulum*. In calculating the defoliation index, the proportionally greater influence heavy defoliation had on plant response was accounted for by squaring each defoliation score. Squared values for each year were added together and divided by the number of years the plant was recorded as living. This created a mean defoliation score as a continuous numeric variable, where overall larger values indicated greater defoliation.

To calculate the defoliation index for survival, the 2002 and 2003 defoliation scores were combined. This was then divided by one for plants found dead in 2003, or two for plants still alive in 2004. Defoliation scores collected during 2004 were excluded from the index calculation, because if the plant was still alive in 2004, any related response (dead or alive) to its current defoliation condition was not able to be observed until a time beyond this project.

The 2003 data was included in the calculations of the defoliation index for relative height change as it closely related to observed height responses. Therefore, if a plant was still alive in 2004, the defoliation index was calculated by adding the squared values of the 2002, 2003 and 2004 defoliation scores, and dividing this figure by the number of years the plant remained alive.

Site variables

Catchment was included as an explanatory variable to test the effect of the treatment (Temple) and non-treatment (Huxley) area on the probability of survival and growth rates of *P. patulum*. While ideally the effects of poison treatment on survival and growth would be tested here, since there is no replication beyond the catchment level, and 'catchment' encompasses all site differences as well as treatment, direct inferences of the effect of poisoning cannot be made. To test how environmental conditions within the study area influenced survival and growth, aspect was combined into two classes (warm or cold), altitude (m), slope (°), habitat (shrubland, forest edge, forest), and site (site) where plants were recorded within each catchment).

Probability of survival

To test how the defoliation index and site variables determined the probability of survival, a binary response variable (alive (1) or dead (0) in 2003 and/or 2004) was used. Since the response variable was binomial, generalised models with binomial errors and a logit link function were used (GLMMs for the mixed models and GLMs for the generalised models). The random effect was non-significant for the probability of survival (using the method outlined above), so GLMs were used to test the influence of the main effects (defoliation index, habitat, aspect, altitude and slope) on the probability of survival. Backwards stepwise selection (the drop1 function in R) was used to determine the minimum adequate model. To test whether catchment explained any additional variation in the model, catchment was added to the minimum adequate model and the significance of the resulting change in deviance assessed.

Growth rate

The response variable for growth rate was a continuous numeric variable created by subtracting the 2002 height from the 2004 height measured for each plant. This variable was log transformed to normalise its distribution (Erickson and Nosanchuk 1992). Linear models (LMEs for the mixed

models and LMs for the fixed effects models) were used to determine which factors best predicted growth. The random effect was again non-significant, so LMs were used to test the main effects of defoliation index and site factors (habitat, aspect, altitude and slope) on the growth rate. Backwards stepwise selection (the drop1 function in R) was used to determine the minimum adequate model. To test whether catchment explained any additional variation in the model, catchment was added to the minimum adequate model and the significance of the resulting change in deviance assessed.

Data analysis mistletoe

Mistletoe data was analysed using the same procedure described for *P. patulum* described above (both species combined). However, after an initial assessment of the mistletoe data, it was decided that measurements for size were unreliable. This was because of the high degree of error associated with size estimates from plants high above the ground. As a result, growth rates of mistletoe were not assessed. The impact of herbivory on the probability of survival was tested instead.

Probability of survival

To test how defoliation index and site variables determined the probability of survival, a binary response variable (alive (1) or dead (0) in 2003 and/or 2004) was used. Since the response variable was binomial, generalised models with binomial errors and a logit link were used (GLMMs for the mixed models and GLMs for the generalised models). The random effect was non-significant for the probability of survival (using method outlined above), so GLMs were used to test the main effects of defoliation index and site factors (catchment (treatment, non-treatment), aspect, altitude and slope) on the probability of survival. Backwards stepwise selection (the drop1 function in R) was used to determine the minimum adequate model.

Foliage cover was not tested as either a response variable or an explanatory variable in the models. This was because it was strongly correlated to the defoliation index, which was considered the variable of most interest.

3. Results

Pre-poison comparisons (2002)

*Age class composition of *P. patulum**

Seedling and sapling plants were the dominant age classes in both the treatment and non-treatment areas. However, there was a more even age class distribution in the treatment area for both seedlings and saplings. In the non-treatment area, saplings made up the vast majority of plants in the sample, and seedlings were relatively scarce (Table 1).

Table 1. Proportions of *P. patulum* plants in each age class in the treatment (Temple catchment) and non-treatment areas (Huxley catchment).

	Seedlings	Saplings	Sub-adults	Adults
Treatment	104 (31%)	164 (49%)	45 (13%)	24 (7%)
Non-Treatment	22 (6%)	304 (81%)	18 (5%)	32 (9%)

A greater number of sub-adult plants were sampled in the treatment area than in the non-treatment area, whereas slightly more adult plants were sampled from the non-treatment compared with the treatment area (Table 1). Adult plants were present at six sites in the treatment area. In comparison, adult plants were found at only two sites in the non-treatment area, indicating that adults may be more widespread in the treatment area than in the non-treatment area.

Defoliation levels

Comparisons between the two catchments in 2002 highlight differences in defoliation levels prior to the initiation of the poison operation. In particular, defoliation of *P. patulum* in the non-treatment area was greater than in the treatment area, with greater proportions of heavy and moderately defoliated plants (Figure 5). Correspondingly, a greater proportion of plants in the treatment area

had either light, or no defoliation. This variation between the two catchments present at the onset of this study has potential implications for some of the results, and will be discussed accordingly.

For mistletoe, there were slightly higher levels of defoliation recorded in the non-treatment area than in the treatment area in 2002, although there was no obvious imbalance between the two catchments (Figure 6).

Changes in defoliation levels between 2002 and 2004

Treatment area (Temple catchment)

Defoliation levels of *P. patulum* declined consistently between 2002 and 2004 (Figure 5). In particular, there were large declines in the heavy, moderate and light defoliation categories. These declines in defoliation were balanced by an almost two fold increase in the proportion of plants recorded as having no defoliation.

One percent of the sample died, and four percent went missing (presumed dead) between 2002 and 2003. However, no further plants died or went missing between 2003 and 2004. This indicates that the initial loss of plants was the result of lag effects from defoliation events that occurred prior to possum control.

A similar pattern of decline occurred for mistletoe in the treatment area (Figure 6). In particular, moderate defoliation declined dramatically between 2002 and 2004. Heavy defoliation remained low for the period. Correspondingly, large increases were observed in the proportion of plants found without evidence of defoliation in 2004. However, nine percent of mistletoe had died by 2004. This may reflect lag effects of possum herbivory in combination with natural attrition.

Overall, the pattern of defoliation between 2002 and 2004 in the treatment area for both *P. patulum* and mistletoe resulted in a predominately one-way shift toward zero defoliation for both mistletoe and *P. patulum*. This result is consistent with the

possibility that plants may have recovered following a reduction in possum numbers.

Non-treatment area (Huxley catchment)

Changes in defoliation of *P. patulum* in the non-treatment area between 2002 and 2004 were varied (Figure 5). Declines in heavy defoliation occurred between 2002 and 2004. Moderate defoliation initially increased slightly between 2002 and 2003 but then declined between 2003 and 2004. Light defoliation levels changed least. Declines in defoliation levels may reflect possum feeding behaviour. Plants may be unattractive to possums when there is little foliage remaining following heavy defoliation events (Coleman *et al* 1985; Nugent *et al* 2000; Allen *et al* 2002).

Declines in defoliation corresponded with an increase in the number of plants that recorded no defoliation, and increasing proportions of plant death. Increasing mortality in the non-treatment area (from 0%, 15%, 19% in 2002, 2003 and 2004 respectively) is in contrast with that observed in the treatment area (0% and <5% in 2003 and 2004 respectively), and was consistent with ongoing herbivory impacts.

Changes in mistletoe defoliation levels in the non-treatment area were consistent with ongoing herbivory. In particular, heavy defoliation (score 4) in mistletoe increased dramatically between 2002 and 2003 (5% to 19%), then declined in 2004 (Figure 6). Moderate defoliation also declined over the study period, which may reflect changes in possum feeding behaviour after a heavy defoliation event. Light defoliation was observed to change least, similar to the pattern observed for *P. patulum*. These declines were balanced by an increase in the number of plants that recorded no defoliation, and increases in plant mortality.

Despite similarities in some responses between the two catchments, contrasting patterns were emerging. In particular, in the non-treatment area there was an emerging pattern of periods of heavy defoliation, followed by an increase in plant mortality, and a proportion being left alone for both *P. patulum* and mistletoe. This result indicates an overall cycle of population decay and decline of these species following herbivory. This pattern contrasts to the pattern observed in the treatment

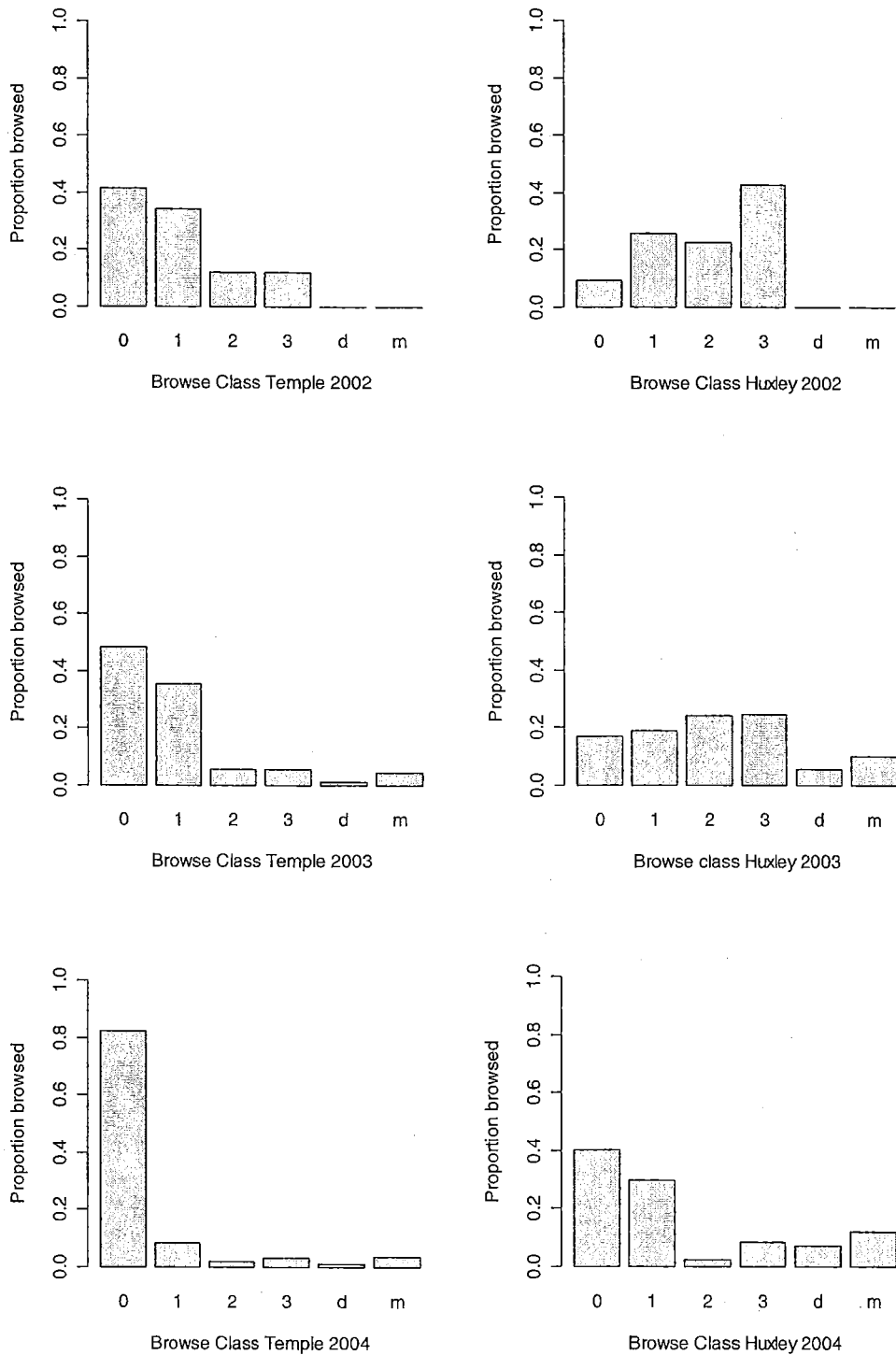


Figure 5: Defoliation levels on *P. patulum* in the treatment (Temple catchment) and non-treatment (Huxley catchment) between 2002 and 2004. Defoliation classes: 0=zero defoliation; 1=light defoliation (1-33%); 2=moderate defoliation (34-66%); 3=heavy defoliation (67-100%); d=dead; m=missing. Possums were poisoned in the Temple catchment after monitoring in 2002.

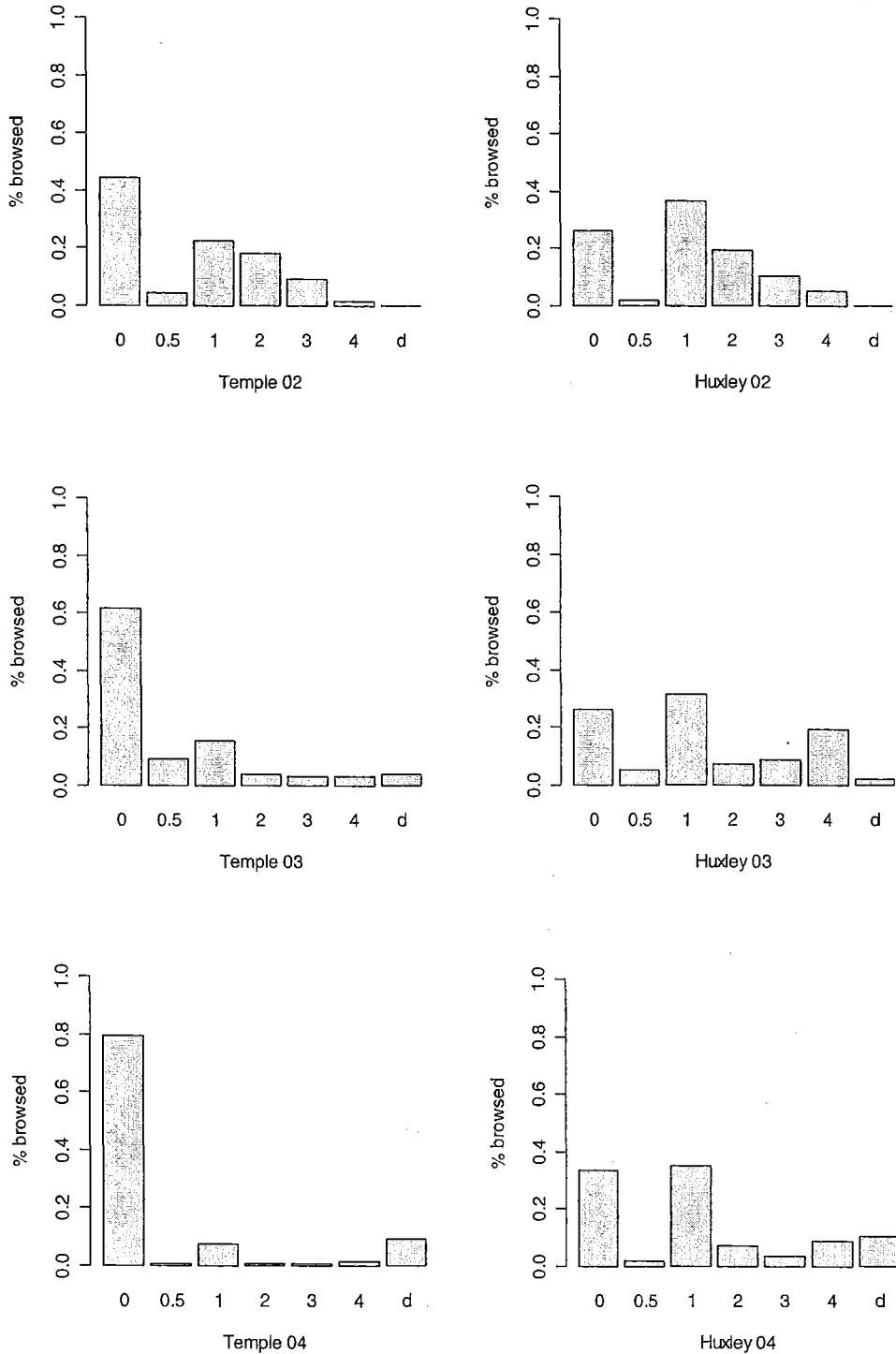


Figure 6: Defoliation levels on mistletoe in the treatment (Temple catchment) and non-treatment area (Huxley catchment) between 2002 and 2004. Defoliation classes: 0=zero defoliation; 0.5=very light defoliation (0.5-<5%); 1=light defoliation (5 -25%); 2=light/moderate defoliation (25%-50%); 3=moderate/ heavy defoliation (51%-76%); 4=heavy defoliation (76%-100%), d=dead. Possums were poisoned in the Temple catchment after monitoring in 2002.

area over the same time period, where mortality and heavy defoliation tapered off over time for mistletoe, and for *P. patulum* ceased all together following possum control.

Age-dependent defoliation effects

In 2002 defoliation effects were evenly spread among all age classes in both catchments. Following possum control in the treatment area, the most obvious changes were a consistent decline in defoliation levels on all age classes in the treatment area. In particular, there was no defoliation observed at all on adult plants in 2004 (Figure 7). Seedlings, saplings and sub-adults remained affected by low levels of heavy and moderate defoliation. The levels of defoliation on these age classes were very low (<5% for all age classes), and may be the result of ongoing impacts from various ground based herbivores.

In the non-treatment area defoliation remained relatively evenly spread among the different age classes. However, there was a trend toward greater levels of defoliation on saplings and seedlings, and this may reflect greater vulnerability of plants in these age classes to herbivory. Alternatively, this trend may reflect a recording bias. Light defoliation may be scored more often on smaller plants, as light defoliation on adult plants is more difficult to observe. However, 90% of the plants that died in the entire study area were seedlings and saplings, indicating a susceptibility of smaller plants to defoliation (Table 2).

Table 2: Percentage of dead *P. patulum* plants in each age class in 2004 in the treatment area (Temple catchment) and non-treatment area (Huxley catchment).

	Seedlings	Saplings	Sub-adults	Adults
Treatment	3%	6%	5%	4%
Non-treatment	48%	23%	6%	14%

Age-dependent defoliation effects were assessed in more detail within the modelling framework discussed below.

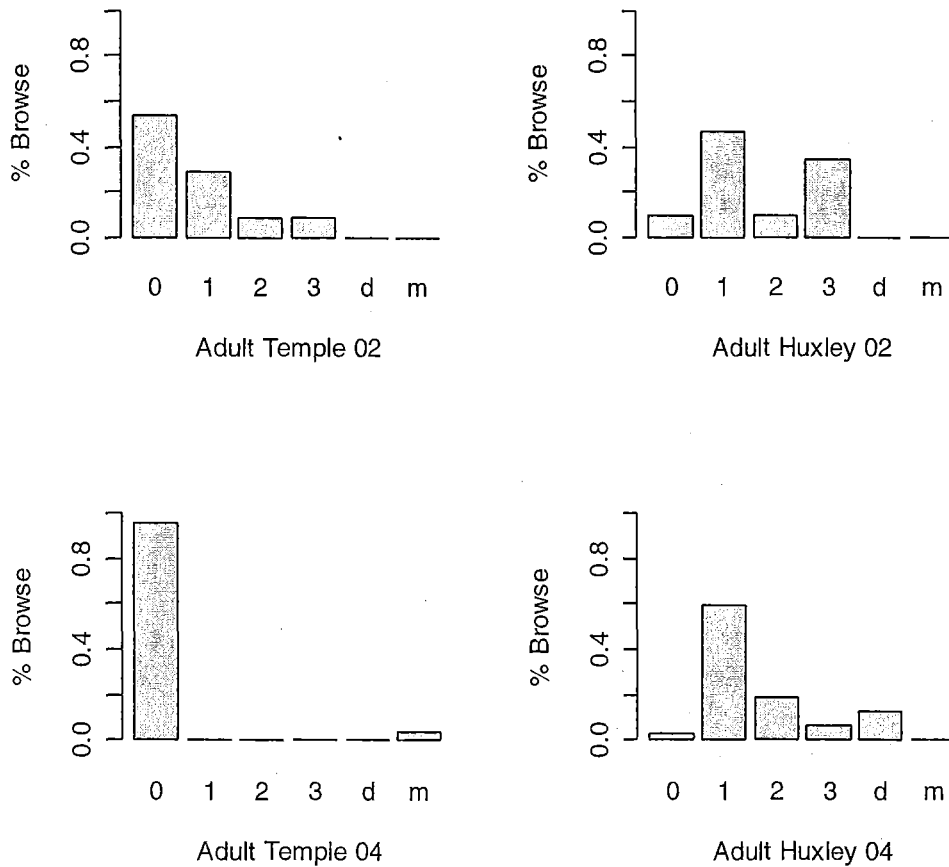


Figure 7: Defoliation levels on adult *P. patulum* in the treatment (Temple catchment) and non-treatment area (Huxley catchment) in 2002 and 2004. Defoliation classes: 0=zero defoliation; 1=light defoliation (1-33%); 2=moderate defoliation (34-66%); 3=heavy defoliation (67-100%); d=dead; m=missing. Possums were poisoned in the Temple catchment after monitoring in 2002.

Changes in mistletoe foliage cover

Contrasting changes in mean foliage cover on mistletoe occurred between the two catchments during the study period. In the treatment area, mean mistletoe foliage cover increased from 62% in 2002 to 69% in 2004. In the non-treatment area, mean foliage cover decreased steadily, from 63% in 2002 to 44% in 2004. These contrasting patterns are consistent with the observed changes in defoliation levels,

where large declines in defoliation on mistletoe in the treatment area were associated with increased foliage cover levels on mistletoe.

P. patulum survival

Following backward selection, four variables were retained in the minimum adequate model explaining *P. patulum* survival: habitat, height, defoliation index and the interaction between height and defoliation index (Table 3a). All four variables remained significant when catchment was included as an additional explanatory variable (Table 3b).

Table 3. General Linear Models showing probability of *P. patulum* survival with binomial errors and logit link function (binary response variable 0, 1). **a.** Results of model excluding catchment effect. **b.** Adjusted model including catchment as an extra explanatory variable. Negative parameters indicate that the probability of survival was less than that of the sub-variable set as the reference category. The change in deviance (ΔDev) on removal of the variable from the model was tested against the X^2 distribution.

a.						
Variable	Category	Parameter est.	SE	ΔDev	p	
df = degrees of freedom						
Habitat (df=2)	Forest	0		20.4	<0.0001	
	Forest edge	-1.145	0.2610			
	Shrubland	-0.3557	0.3632			
Defoliation index: height interaction (df=1)		-0.000270	0.0000540	29.7	<0.0001	
	Defoliation index	0.1392	0.05998			
	Height	0.001613	0.000330			
b.						
Habitat (df=2)	Forest	0		12.5	0.00190	
	Forest edge	-0.6910	0.2761			
	Shrubland	-1.242	0.4525			
Catchment (df=1)	Huxley	0		18.8	<0.0001	
	Temple	1.704	0.4245			
Defoliation index: height interaction (df=1)		-0.000270	0.0000570	29.6	<0.0001	
	Defoliation index	0.2076	0.06403			
	Height	0.001853	0.0003600			

The significant interaction term implies that the effect of defoliation varies depending on plant height. This is shown in Figure 8, where expected survival is plotted as a function of the level of defoliation at four heights that are representative of seedlings (300 mm), saplings (1500 mm), sub-adults (2500 mm) and adults (4000 mm). Seedlings were found to have a relatively low probability of survival regardless of defoliation level and there was no evidence that higher levels of defoliation reduced survival (the opposite appears the case), suggesting that other factors may play a key role in seedling survival. For the remaining height classes, survival probabilities were high with no or light defoliation, but declined with increasing levels of defoliation. This decline was more dramatic among adult trees. Therefore it appears that tall plants are much more susceptible to dying from heavy defoliation than smaller plants, and that seedlings have relatively high levels of mortality independent of the level of defoliation.

The effect of habitat in the model varied depending on whether or not catchment was included. Without catchment included in the analysis (Table 3a), the probability of death was higher on forest edges compared to shrublands, which was the second most vulnerable habitat. With the inclusion of catchment into the model, plants in shrubland habitat had a higher probability of mortality (Table 3b). Plants in forest habitats were least likely to die, with or without the effect of catchment. The sensitivity of habitat to the effect of catchment when added to the model suggests that there are important unmeasured differences between the two catchments, and that having accounted for these differences, shrubland sites in the treatment are strongly associated with plant death. Although this may be biologically significant, there may be sampling bias toward shrubland habitats in the treatment area compared to the non-treatment area. Consequently, caution is required when interpreting these results as they may not be a precise reflection of habitat vulnerability over the entire study area.

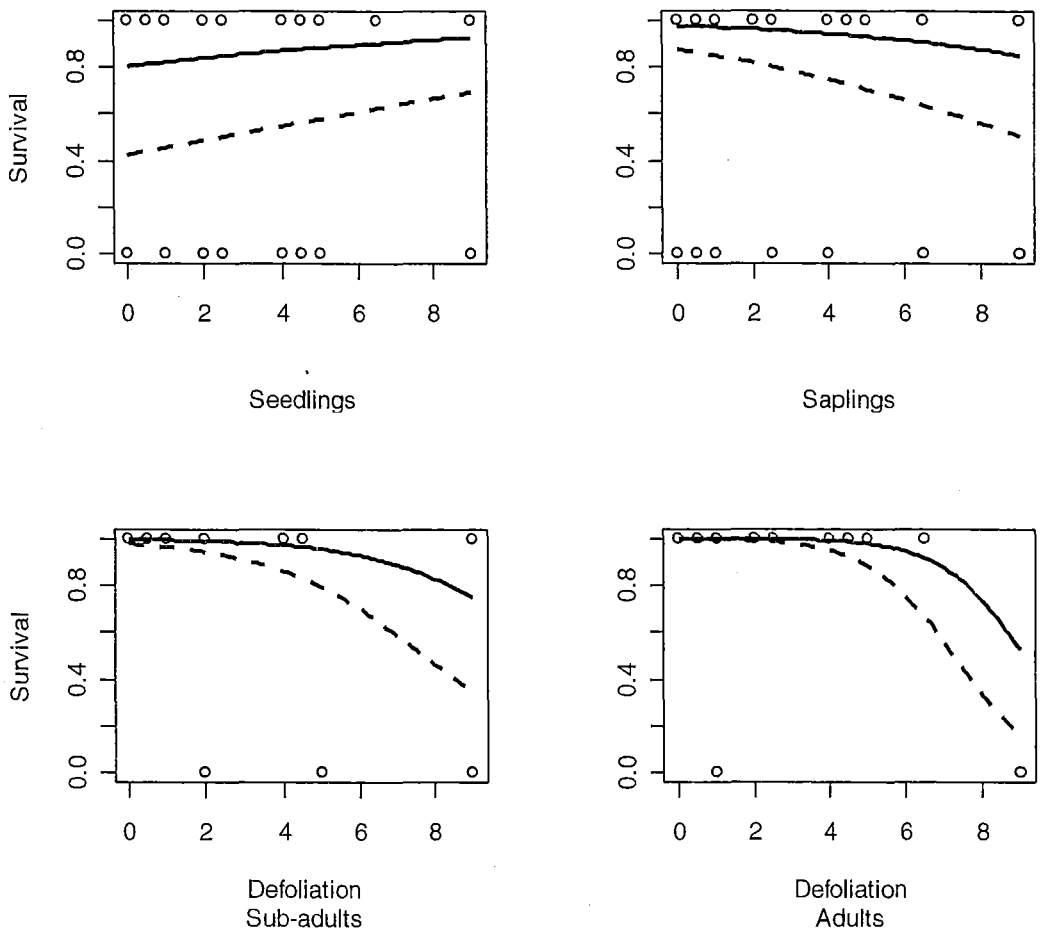


Figure 8: Probability of survival plotted against defoliation for *P. patulum* age classes (seedling (300 mm), sapling (1500 mm), sub-adult (2500 mm), adult (4000 mm)), in shrubland habitats in the treatment (Temple catchment) and non-treatment (Huxley catchment) area, fitted using GLMs (see Table 3a). In all cases the probability of death was greater in the non-treatment area (dashed line).

Including catchment into the model revealed a strong positive effect on survival in the treatment area compared to the non-treatment area (Table 3b). Although this is consistent with a treatment effect, this result is also confounded by a lack of replication and the different background levels of defoliation between the catchments present at the onset. The sensitivity of some of the explanatory variables in the models highlights this. As a result, the catchment effect only provides anecdotal support for a positive treatment effect.

Relative growth rates of *P. patulum*

Following backward selection, only the defoliation index was retained in the minimum adequate model explaining *P. patulum* growth rates (Table 4a).

Table 4: Change in relative growth rates (response variable) of *P. patulum* between 2002 and 2004, fitted using a Linear Model. a. Results of model excluding catchment effect. b. Adjusted model including catchment as a fixed effect. *F*-tests were carried out for all variables removed from the model one at a time.

Variable df = degrees of freedom	Category	Parameter est.	SE	F	<i>p</i>
a.					
Defoliation index (df=1)		-0.004254	0.002070	4.8295	0.02833
b.					
Defoliation index (df=1)		-0.004254	0.002070	4.8295	0.593
Catchment (df=1)				7.3975	0.0067
	Huxley	0			
	Temple	0.031912	0.01173		

The effect of defoliation on growth rates is shown in Figure 9. This plots growth rates as a function of the level of defoliation. The negative relationship between defoliation levels and growth rate is consistent with the removal of plant biomass from herbivory. With the inclusion of catchment into the model, defoliation index became non-significant (Table 4b), and catchment became the most significant variable explaining relative growth rates of *P. patulum*.

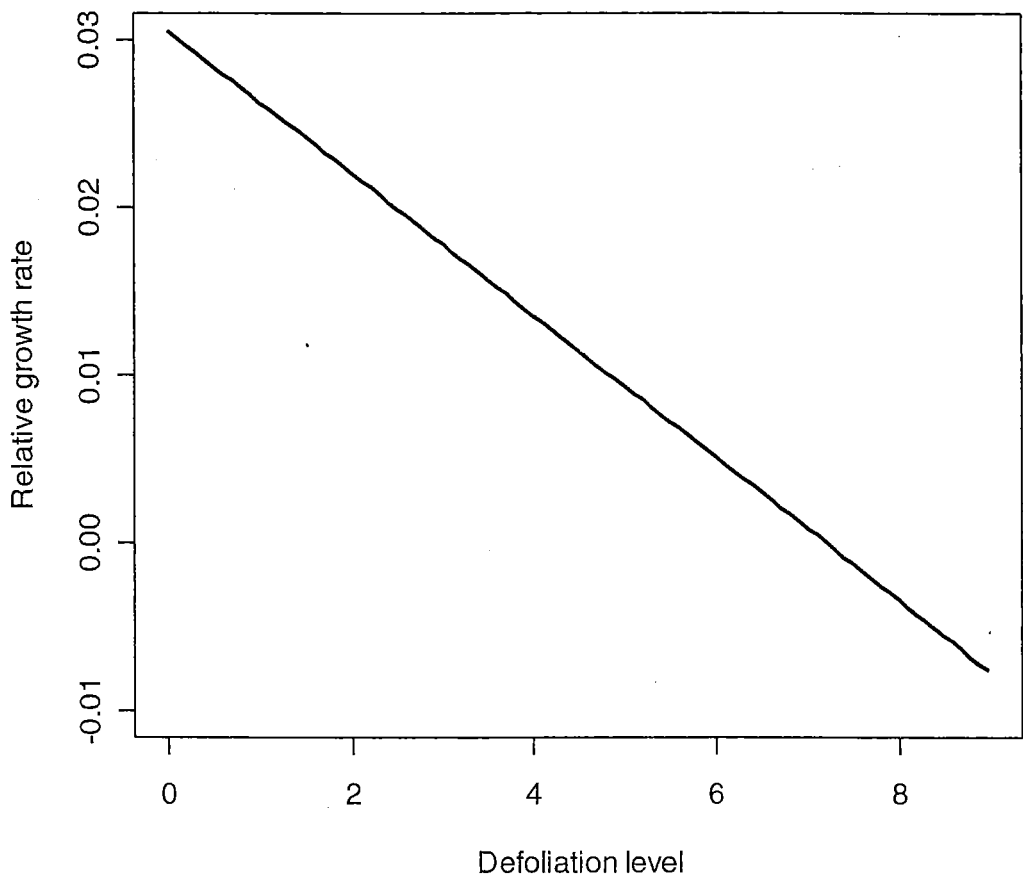


Figure 9: Relationship between relative growth rates of *P. patulum* and defoliation levels fitted using Linear Models.

The higher growth rate of plants in the Temple catchment is consistent with a treatment effect due to possum removal. Alternatively, it may also reflect a more suitable environment in the Temple for plant growth. If the latter were correct, we could expect environmental variables such as habitat, slope, altitude and aspect to explain significant variation when fitted in the model that includes catchment. When catchment was fitted in the model that included site variables (but excluded defoliation index), plant growth was positively influenced by warm aspects in the treatment area, which indicates a preference for growth and/or higher densities of possums on warm aspects. However, no other site variable in the treatment area influenced plant growth in the treatment area. Hence the positive influence of

warm aspects on growth provides tentative support for a climatic difference between the two areas, and weakens evidence of a treatment effect.

Mistletoe survival

By way of backward selection, four variables were retained in the minimum adequate model explaining mistletoe survival: defoliation index, altitude, slope and aspect. Defoliation was the most significant predictor of mistletoe survival (Table 5). In particular, the probability of death increased with higher levels of defoliation, which is direct evidence of herbivory impact. The probability of survival was influenced by several environmental predictors. The most significant of these was slope, with mortality increasing with steeper slopes. Altitude and aspect were also both significant predictors of survival, with the mortality being greater at lower altitudes and warm aspects. Catchment did not affect mistletoe survival when fitted in the full model with other variables, or as an explanatory variable on its own. This suggests that killing possums in the treatment area has had little measurable effect on the probability of mistletoe death to date.

Table 5. Results of General Linear Model for the probability of mistletoe survival with binomial errors and logit link function (binary response variable 0, 1). The change in deviance (*ΔDev*) on removal of each variable from the model was tested against the χ^2 distribution.

Variable (df)	Category	Parameter est.	SE	<i>ΔDev</i>	<i>p</i>
Defoliation index (df=1)		-0.238671	0.062536	15.7	<0.0001
Aspect (df=1)	Cold	0		6.0	0.01455
	Warm	-1.544801	0.641185		0.015984
Altitude (df=1)		0.007264	0.003311	6.4	0.011647
Slope (df=1)		-0.079384	0.031541	7.3	0.006959

The effect of these variables on the probability of mistletoe survival is shown in Figure 10. Expected survival is plotted as a function of the level of defoliation for plants on warm aspects at four different altitudes (1000 m, 900 m, 800 m and 700 m) representing different survival probabilities. Plants at higher altitude (1000 m

and above) had a relatively low probability of death regardless of defoliation level when compared with plants at lower altitudes.

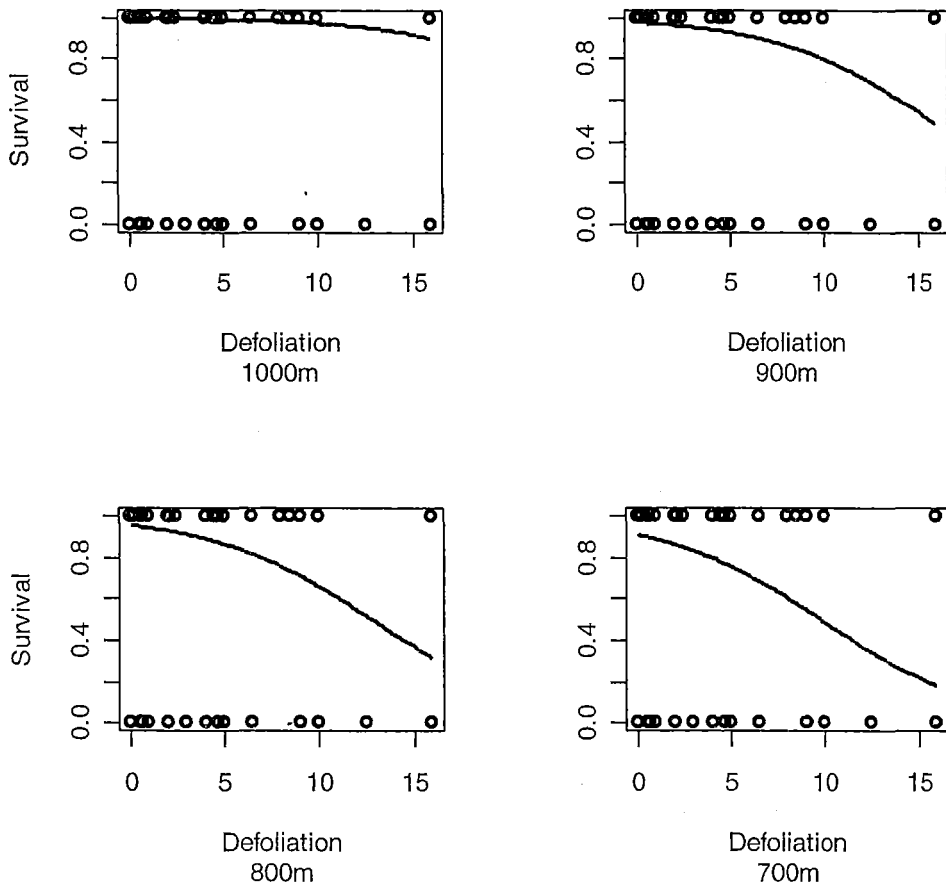


Figure 10: Probability of survival for mistletoe plotted against defoliation index for plants on warm aspects and at 10° slope at 4 different altitudes (1000 m, 900 m, 800 m and 700 m abs), fitted using GLMs (see Table 5). Probability of death increases with lower altitude.

4. Discussion

Impact of herbivory

This study provides direct evidence that herbivory is a major threat to *P. patulum* and mistletoe in the Temple and Huxley valleys of the South Island, New Zealand. In particular the results demonstrate that heavy herbivory will cause premature death of these species, and has a negative effect on the growth of *P. patulum*. Consequently possums pose a significant threat to the long term survival of these species.

This study supports previous research demonstrating a link between mistletoe condition and possum herbivory (Rance and Rance 1996; Sessions 1999; Sessions *et al* 2001). The decrease in mistletoe foliage cover between the treatment and non-treatment area observed in this study reflects a response to herbivory that is consistent with studies on this species in similar forest types (Sessions *et al* 2001).

Few studies have drawn firm conclusions on whether possum herbivory leads directly to mortality. Rather, mortality has been assumed to be the logical end point following declining mistletoe condition resulting from possum herbivory. A key finding of this study was the direct link between defoliation levels and mistletoe death.

No previous studies have attempted to quantify impacts of possum herbivory on *P. patulum*. Although possum damage is considered the major factor contributing to the decline of *P. patulum*, this was based largely on anecdotal records and field reports (Rogers and Walker 2005). The results from this study demonstrate that browse by possums is a major factor contributing to *P. patulum* mortality. Consequently, possums

pose a significant and real threat to the long term conservation of this species.

The finding that larger (adult) *P. patulum* plants were more likely to die from heavy defoliation than smaller plants is a significant outcome for the conservation of this species. This provides direct evidence that adult plants are targeted and subsequently killed by possum browse. In addition, it supports anecdotal claims that possums are responsible for the widespread loss of adult *P. patulum* from throughout the species range wherever possums have been present for long periods of time.

Adults may have a limited capacity to recover from heavy defoliation, as indicated by the steep decline toward death with increasing defoliation levels. However, the ability of adult plants to recover from heavy defoliation remains largely unknown. Field evidence suggests it is limited and/or slow. Although re-sprouting was observed on many plants, typically a heavily defoliated plant remained defoliated for the period of this study (pers. obs.). It has been suggested that the stress of heavy herbivory leaves plants vulnerable to fungal attack and disease, which in turn compounds the stress from herbivory (Crawley 1983; van Eynhoven and Norton 1999; Allen *et al* 2002). In addition, these impacts would be more pronounced in harsh environments of climatic extremes typical of the study area, and/or on plants that are approaching natural senescence. Although this could not be quantified, any combination of the afore-mentioned factors may explain the inability of heavily defoliated adult plants to recover from heavy defoliation.

Alternatively, plants may be visited too regularly by possums to allow successful recovery to occur. Visits by possums are likely to be more regular in low diversity forest types where the pressure on palatable species is greater (Owen and Norton 1994). For *P. patulum*, it would not require many visits to maintain a state of heavy defoliation and prevent recovery. However, determining the rate at which this occurs would require more frequent monitoring. Therefore assumptions of slow

recovery rates in *P. patulum* may reflect the inability of the monitoring regime to detect intermediate defoliation events that are maintaining a state of degradation in adult plants.

Defoliation levels were less important predictors of mortality in smaller plants. This finding may be the result of a recording bias toward adult plants due to longer lag periods between heavy defoliation events and mortality of larger plants. This ensures the history of defoliation leading up to death is recorded. Conversely, heavy defoliation of smaller plants was more likely to be missed, due to smaller plants being disproportionately more vulnerable to one-off heavy defoliation events from numerous mammalian herbivores. A chance encounter between small plants and any number of mammalian herbivores is likely to result in immediate death, such as decapitation, or being completely stripped of foliage (Rogers and Walker 2005). Subsequently, a heavy defoliation event on small plants may be unnoticed following the previous years' score and its mortality.

The potential impacts of herbivory on smaller plants should not be dismissed, as indicated by the higher probabilities of mortality for small plants. This is further confirmed by the larger proportions of smaller plants that died during the study period. Rogers and Walker (2005) provide support for this scenario. Although their study did not follow the plight of individual plants, their assessment of defoliation levels on the different age classes of *P. patulum* found that seedlings and saplings were the most defoliated age classes. They attributed this to exposure of small plants to a wide range of ground dwelling herbivores. In addition, they found that while adult plants were generally the least defoliated of the age classes, these were more likely to be heavily defoliated. Rogers and Walker (2005) attributed the heavy defoliation of adults to selective targeting by possums, being the only arboreal herbivore capable of this impact. The results from this study confirm this suggestion.

These results provide insight into the vulnerability of the different life stages of *P. patulum*. It has been suggested that small plant size ensures a reduced threat from selective feeding by possums due to low visibility. However, this is countered by being exposed to a greater range of ground based mammalian herbivores and the higher probability of mortality from one-off random encounters. On the other hand, although adult plants are largely free from most ground based herbivores, they are heavily targeted by possums because they are highly visible and a preferred food resource. This also ensures a high probability of death.

Paradoxically, small plants remain in relative abundance throughout the species natural range (van Eyndhoven and Norton 1999), which suggests that small plants are more resilient to herbivory than adults. The results of this study shows that while adults may be the first to be eliminated from the population, no stage in the life cycle of *P. patulum* is free from debilitating herbivory. This has serious consequences for the long term sustainability of this species, as discussed later. It also raises questions about the dynamics of the seedling life cycle.

Environmental influences

The results from this study provide insight into the complexity associated with attempts to quantify possum impacts, and why many previous studies have struggled to adequately predict such impacts.

Mortality of *P. patulum* was higher in non-forest habitats (shrublands and forest edges), compared to forest habitats (under canopy). A logical explanation for this is that possum numbers are higher in these habitats. Studies have shown that possum densities are greater in habitats that have more abundant food resources (Coleman *et al* 1985; Nugent *et al* 2002). Fittingly, plant diversity is relatively high in shrublands and includes a number of species attractive to possums, such as snow totara

(*Podocarpus nivalis*) (Coleman *et al* 1985). In contrast, food resources under mountain beech forest in the study area were scarce, and few vascular plant species were present other than mountain beech. Consequently, the greater abundance of possums in shrubland habitats, in combination with *P. patulum* being a highly targeted species, increases the probability of mortality in these habitats.

Shrublands may also allow possums to access *P. patulum* otherwise out of reach. For example, shrublands form a dense canopy that can support the weight of a possum. This provides a platform for possums to access emergent *P. patulum*. In particular sapling and sub-adult plants would be vulnerable. These age classes are otherwise considered safe from possum impacts because they are tall enough to avoid ground herbivory, but too slim to support the weight of a possum, and sufficiently rigid to prevent being bent down and eaten (Rogers and Walker 2005). Possum faeces were regularly observed on the shrubland canopy near dead and degraded *P. patulum* (pers.obs.) providing support for this scenario.

Rogers and Walker (2005) highlighted an absence of *P. patulum* from shrublands in northern populations. They correlate this absence to the long history of possum presence in these areas. The vulnerability of *P. patulum* in shrubland habitats highlighted in this study may explain why *P. patulum* is scarce in these habitats today. Correspondingly, *P. patulum* is still relatively common in shrubland habitats in the study area because possums are a recent arrival compared to northern areas (Cowan 1990; Clout and Ericksen 2000). This scenario is also consistent with the loss of adult plants from northern populations, which is also attributable to the long presence of possums.

In addition, habitat susceptibility may reflect exposure to extreme events. Shrublands and edge habitats are more exposed to snow fall damage, compared to sites under forest (although the latter is more prone to windfall damage). Interestingly, the probability of *P. patulum* mortality also increased with steeper slopes. This may support an environmental

disturbance effect given that steeper slopes are more prone to some disturbance events, such as avalanche and landslide, although no disturbance at this scale was noted during the period of the study.

Although there may be some biological relevance to the results discussed above, these results are inconsistent and caution is required in their interpretation. For example, because defoliation levels had a direct influence on plant growth and survival of *P. patulum*, it seems reasonable to expect a consistent effect of site variables on these responses. Although the probability of survival was influenced by habitat type discussed above, habitat type had no influence on growth rates. Whereas growth rates were positively influenced by warm aspects, but warm aspects had no influence on survival. This inconsistency highlights the randomness associated with possum impacts, as well as problems associated with a lack of replication. The latter in particular, partly explains the inconsistency between environmental variables and responses.

Mistletoe survival was also influenced by environmental variation. In particular, probability of death increased on steep slopes, with warm aspects and at lower altitudes. These results may reflect possum preferences to local environmental variation. For example, it may be that the interaction between altitude, slope and warmth provide better growing conditions for mistletoe and plants generally. More abundant food resources and corresponding higher possum densities ensures a greater chance of herbivory on preferred species. With mistletoe, catchment had no influence on the relative significance of these variables, which implies greater confidence in these results. Nevertheless, attributing logical biological explanations to these effects remains difficult unless numerous related variables are measured and quantified (Sessions and Kelly 2001b). Overall, these results highlight why studies have struggled to predict possum impacts.

Catchment effect

A key part of this study was to compare the different responses of *P. patulum* and mistletoe between catchments with different possum control histories. The assumption was that if possums were a major herbivore impacting on *P. patulum* and mistletoe, any observed recovery in the treatment area would be consistent with a possum defoliation impact. It would also be an indication of the effectiveness of the control operation.

Because this study showed that defoliation had a direct negative impact on plant survival and growth, by inference removing possums from an area benefits these palatable species. Fittingly, in all cases plant survival and growth improved in the treatment area compared to the non-treatment area, which is highly indicative of a treatment effect. However, although these responses meet the expectations of a treatment effect, caution is required in their interpretation. In particular, these responses are influenced by pre-existing differences between the two areas in 2002. This is further complicated by a lack of replication, and the possibility that unmeasured variables may have influenced the catchment effect.

For example, the different background levels of defoliation between the catchments in 2002 were likely to have influenced survival rates. In particular, the greater proportion of heavily defoliated *P. patulum* in the non-treatment area indicates that a greater proportion of these plants would likely die regardless of any further defoliation. The greater proportion of death in the non-treatment area following 2002 may be in part attributed to this background lag effect.

The influence of lag effects is also observed for mistletoe. The background levels of defoliation in mistletoe were similar in the two catchments, and differences in the proportions of dead plants between the two areas were much less (although a greater proportion of plants died in the non-treatment area). For this reason, catchment was not

found to be a significant predictor of mistletoe survival. The similar mortality level observed in the two catchments, despite possum control having occurred in the treatment area, is attributed to lag effects rather than an indication of ongoing herbivory. Alternatively, this result challenges the findings of some studies that have suggested mistletoe is an effective indicator species to possum herbivory (Sessions *et al* 2001). Overall, this highlights that longer term data is required to more accurately assess the influence of possum control on the survival of *P. patulum* and mistletoe.

Other positive responses in the treatment area were less influenced by lag effects. The much greater growth of *P. patulum* in the treatment area was an example of this. Lag effects are less likely to influence growth rates because the impact of herbivory is likely to be more immediate (unless a plant is near death). Therefore it could be argued that the positive response in plant growth in the treatment area is evidence of a treatment effect.

An alternative explanation for the difference in plant growth between the two catchments is that the treatment area has a better climate for plant growth, or that there is some other unmeasured variable unrelated to possum impacts exerting an effect. Although it seems unlikely that climates would be significantly different given the proximity of the two areas, there was an indication of a climatic preference for plant growth. For instance, warm aspects in the treatment area strongly influence plant growth. Although this does not negate a treatment effect, especially if warm sites are favoured by possums, it does indicate a climatic preference operating in the treatment area, and weakens the strength of a treatment effect. The upper Huxley also appears to have higher rainfall, as indicated by the presence of silver beech.

The observed change in mistletoe foliage cover, however, provides firm support for a treatment effect. Foliage cover increased in the treatment area following possum control. This was clearly contrasted by a decline in

foliage cover in the non-treatment area. This response is consistent with other studies that show rapid recovery of mistletoe foliage after the removal of possums (Sessions and Kelly 2001b). For this reason, mistletoe are used as indicator species (Sessions *et al* 2001). The response observed in this study is therefore highly indicative of a treatment effect.

Overall, the varying catchment effect provides a good example of the complexities underlying defoliation impacts between different but environmentally similar areas. From the beginning of this study, monitoring data highlighted evidence of population decline and decay present in both the treatment and non-treatment areas. Heavy browse was commonly observed on mistletoe and *P. patulum*. The non-treatment area in particular, was more damaged by 'possum' browse. However, RTC rates for both areas were similar indicating similar possum densities.

There are two possible explanations for the difference in browse impact between the treatment and non-treatment areas. Firstly, the treatment area has large areas of induced grassland in the lower valley. This may serve as an alternative and preferred food resource, given an abundance of nutritious exotic herbs such as white clover (*Trifolium repens*) (Coleman *et al* 1985; Sweetapple and Nugent 1998; Nugent *et al* 2000), and would alleviate browse pressure on forest and shrubland habitats. Secondly, during the 1970s extensive rabbit control using 1080 carrot bait was undertaken in the treatment area (Canterbury Regional Council records). This may have suppressed the possum population - albeit a very new and probably small population.

Furthermore, possums are a relatively recent incursion to these valleys, and are yet to reach peak densities (Cowan 1990; Clout and Ericksen 2000). This may explain why there is an abundance of *P. patulum* and mistletoe in the Ohau catchment. These reasons may explain why the treatment area contains healthier populations of *P. patulum* and

mistletoe, compared to the non-treatment area where there has been severe recent browse pressure on these species.

Patterns of defoliation and long term trends

Assessment of defoliation levels between the two catchments over the period of this study provides further insight into the impacts of herbivory on *P. patulum* and mistletoe. What is particularly useful is the change in defoliation levels over time, as it allows for the assessment of plant/herbivore trends. It also provides an indication of treatment success.

Accordingly, the changing defoliation levels observed in this study provide some evidence of a treatment effect. The universal decline in defoliation levels and reduced mortality for both mistletoe and *P. patulum* in the treatment area are consistent with recovery following a release from herbivory (Stewart and Veblen 1982; Payton *et al* 1997; Norton 2000; Sessions *et al* 2001; Sessions and Kelly 2001b; Nugent *et al* 2002; Sweetapple *et al* 2002).

The response in the non-treatment area reflects a different trend. Although declines in heavy defoliation occurred in the non-treatment area, these may reflect high seasonal and random possum feeding behaviour (Sessions and Kelly 2001b). For example, this pattern is consistent with studies that have shown possums selectively browse palatable species until they become an energetically inefficient resource, i.e. not worth the effort. Plants are then ignored by possums until they have recovered sufficiently to become a worthy target again (Owen and Norton 1994; Pekarharing *et al* 1998; Nugent *et al* 2000). Fittingly, this cycle of declining heavy defoliation levels in the non-treatment area is matched by increasing proportions of dead plants that were unable to recover. Contrasting trajectories of sustainability for *P. patulum* and mistletoe are therefore emerging in the treatment and non-treatment area.

The changing pattern in defoliation levels between the two catchments also demonstrates the difficulty in determining cyclic trends with short term monitoring data. This is highlighted by similarities in the response of defoliation levels between the two catchments. Although the declines in heavy defoliation in the non-treatment area could conflict with a key hypothesis of this study, careful interpretation reveals a pattern that is consistent with severe possum impacts. Potential confusion arises because short term data captures only a small segment of a longer term trend. This can result in spurious similarities to contrasting responses depending on what part of the cycle has been monitored.

Long term sustainability – extinction!

The results presented here provide strong evidence of a high degree of threat to palatable rare species (*P. patulum* and mistletoe) in low diversity plant communities. In particular, possum-induced death is causing population degradation and decline, which is indicative of a path toward extinction (Crawley 1983; Bellingham *et al* 1999).

For species that are widely and randomly dispersed throughout large areas of relatively intact habitat, such as mistletoe, the threat of extinction is less certain. The most likely scenario for mistletoe is that as plants become scarce and more degraded by herbivory, natural population functioning will be interrupted (Crawley 1983). The resulting decline or loss of seed production, recruitment, and plant vigour may ultimately lead to extinction (Crawley 1983; Bellingham *et al* 1999; Allen *et al* 2002). Alternatively, mistletoe may persist at much reduced densities on sites inaccessible to possums. Despite studies highlighting a possum threat to mistletoe, including this study, many mistletoe populations remain healthy despite long term possum presence (Owen and Norton 1994; Sessions *et*

al 2001). Fully quantifying the long term threat of browse to mistletoe populations is therefore difficult and imprecise at best.

For *P. patulum*, there is strong evidence of a consistent pattern of decline throughout its natural range, which closely corresponds with possum presence (Cowan 1990; Clout and Ericksen 2000). This wider pattern of loss in *P. patulum* is consistent with the results of this study, with adults (as well seedlings and saplings) being systematically removed from the population by herbivory. The consequences for the sustainability *P. patulum* are serious without intervention.

This indicates that *P. patulum* is more predisposed to extinction than mistletoe, and this is likely to be due to a number of biotic factors. In particular, the morphology of adult *P. patulum* means that possums can easily gain access to *P. patulum* foliage. In addition, an adult plant can easily support the weight of a possum in its crown, making it an effortless and abundant food resource. Total defoliation of adult *P. patulum* was regularly observed over the period of this study which supports this. In contrast to this, many mistletoe plants are in precarious positions on host trees, such as on the extremities of host branches, which mean access to some mistletoe plants is difficult for possums.

Differences in mortality resulting from heavy defoliation between *P. patulum* and mistletoe may reflect the different physiological responses of the species. In particular, mistletoe has been shown to recover relatively quickly following herbivory (Sessions *et al* 2001; Sweetapple *et al* 2002). Observed recovery of *P. patulum* following defoliation appears slow, although capacity for full recovery remains largely unknown. The permanent loss of adults in most populations supports the notion that they have poor recovery potential following heavy defoliation. In addition, given that *P. patulum* is considered to be relatively fast growing (Rogers and Walker 2005), plants could be expected to recover following possum browse. This lack of observed recovery may indicate a particular sensitivity of *P. patulum* to defoliation.

The different habitat requirements of the two species may also influence the relative vulnerability of *P. patulum* and mistletoe. The more specific habitat requirements of *P. patulum* mean that plants are usually clustered together in discrete sites (Rogers and Walker 2005). By comparison, mistletoe in the study area is randomly spread throughout the forest. This clustering makes *P. patulum* a more obvious target, and an energetically more desirable resource than mistletoe. In addition, *P. patulum* is found only in 'low diversity' ecosystems, where the relative pressure on palatable species is greater (Owen and Norton 1994). Mistletoe is more widespread and is found in relatively resource-rich forest types (Norton 1997). In forest types that have more plentiful food sources, possums more readily switch food preferences and are less likely to target one species as frequently (Pekelharing *et al* 1998; Nugent *et al* 2000). This partly explains why long term herbivory impacts on mistletoe have been inconsistent and difficult to predict (Owen and Norton 1994).

In addition, all life stages of *P. patulum* are vulnerable to a range to mammalian herbivores. This study has demonstrated that small plants of *P. patulum* are vulnerable to mortality. The vulnerability of juvenile *P. patulum* to a range of mammalian herbivores adds further stress to the overall sustainability of natural population cycles (Crawley 1983). Mistletoe, however, is generally safe from ground based herbivores when above approximately 2.5 m in height.

Conservation implications

Given the sensitivity of adult *P. patulum* plants to possum herbivory, and the key role adult plants play in sustaining species through the production of seed, introduced possums are clearly the major threat to the sustainability of *P. patulum*, and have considerable impacts on mistletoe.

A key objective of the recovery plans for *P. patulum* (and mistletoe) is to restore healthy and functioning populations across the natural range of these species (Townsend 1999; Dopson 2001). The Ohau catchment contains the most abundant and healthy populations of *P. patulum* in New Zealand, and includes large populations of mistletoe. Unfortunately these populations are under threat from possum herbivory. Maintaining and improving the condition of these populations is a significant priority for conservation because they are the last 'representative' populations of these species, including the only area where significant adult plants of *P. patulum* remain.

Of additional concern for managers of the Ohau catchment is that possum numbers are considered to be at pre-peak densities (Cowan 1990; Clout and Ericksen 2000). This is indicated by the very high RTC rates for the area. Very high possum numbers in these catchments has significant implications for the long term sustainability of the already degraded *P. patulum* and mistletoe. This is especially true as competition for resources increases (Parkes 1994; Forsyth *et al* 2000). As demonstrated by this study, adult *P. patulum* are at particularly high risk of mortality from possum herbivory. In this regard, like mistletoe, adult *P. patulum* are good indicators of the impacts of possums on these ecosystems. As an indicator species, they highlight widespread and severe possum impacts occurring in the Ohau catchment, and illustrate the risk of possums to ecosystems in general. The level of degradation observed on *P. patulum* within this study indicates a high risk of mortality unless management of the substantial possum populations are forthcoming.

Consequently, possum control in the Ohau catchment is necessary to maintain 'functioning' populations of *P. patulum* and mistletoe beyond the treatment area. Unfortunately, other than maintaining possum numbers as low as possible, there is no established density threshold managers can use to ensure the protection of vulnerable species and plant communities generally (Allen *et al* 2002). This is in part due to the

inherent variation present within plant communities, and their corresponding vulnerability to herbivory, as demonstrated by this study, and due to the heterogeneity of possum browse events (Sessions and Kelly 2001b). However, adopting a similar approach used in the treatment area is a cost-effective technique to protect populations of *P. patulum* and mistletoe at the appropriate ecosystem scale. This in turn has benefits to wider ecosystem function and health.

Outside of the Ohau catchment, such is the severity of loss of adult *P. patulum* that seed production and seedling recruitment is now limited. The sustainability of northern populations now depends on immature plants reaching reproductive maturity. However, this study has also shown that small plants are vulnerable to attrition, and it is unlikely that younger plants will reach maturity in the presence of a suite of mammalian herbivores.

This scenario highlights dire consequences for northern populations; that is, without intensive intervention populations will continue to decline. In turn, as populations decrease in size, they become more vulnerable to extinction from environmental stochasticity (Crawley 1983; Gaston 1994; Lesica and Allendorf 1992). In many ways populations that are now devoid of reproducing adults are functionally extinct unless intensive and ongoing management occurs (Duncan and Young 2000).

In northern populations, the restoration of adult plants is considered the most pressing management need. Exclusion of key populations of *P. patulum* from all herbivores is the only realistic option available to achieve this given the degree of loss and complex levels of threat. Strategic fencing around core/discrete populations to exclude mammalian herbivores, in combination with possum control methods such as poison, is probably the most appropriate method to ensure the natural succession of juveniles through to maturity.

The approaches outlined above would also provide valuable research opportunities. Of particular importance to the conservation of *P. patulum* are understanding factors that influence the reproduction and recruitment potential of *P. patulum*. This requires research on germination, dispersal, seed longevity, and recruitment. In addition, although the threat of herbivory to *P. patulum* is clear, a greater understanding of ground based herbivory is desirable. Accordingly, these research themes are identified as priorities in the recovery plan for *P. patulum* and are also consistent with the research priorities for mistletoe (Townsend 1999; Dopson 2001).

Review of monitoring

This study is a good example of the need to balance sound scientific principals of experimental design with the practical realities of ecosystem management. In particular, the significant findings of this study indicate that important results can be gained without meeting the rigours of fully replicated study designs.

Although the lack of replication in this study weakened the amount of inference that could be attributed to some results, especially environmental predictors, the concerns of low replication are disputable. In reality, adequate replication could not be achieved for this study. The expense required to fully replicate the representative range of habitats at the catchment scale throughout the species range would be prohibitive and unmanageable. In addition, the fact that adult plants are missing from populations outside the Ohau catchment questions the usefulness of such replication. Furthermore, alternative approaches, such as poison/non-poison 'block' design within a catchment, would be impossible given possum movement; whereas establishing numerous herbivore exclosures would be difficult and expensive, and tree banding would be physically difficult and an impractical solution at the ecosystem scale.

The key to the success of this study was measuring variables that accurately reflected herbivory impacts that were relevant to the questions being asked. For the purposes of this study, we were primarily interested in growth rates and mortality as the most accurate and crucial responses to herbivory. As such, defoliation scores were an important explanatory variable when applied to individual plants over time. Although the effectiveness of defoliation scores when used in plant canopies has been queried (Payton *et al* 1999; Allen *et al* 2002), this study was able to accurately assess defoliation of *P. patulum* because it is a relatively low growing tree and all plants could be reached.

Sessions and Kelly (2001b), in their investigation of possum and invertebrate herbivores on mistletoe, show that defoliation scores can be influenced by insect herbivory. Although clearly insect damage is different from possum impacts, separating out these differences could be extremely difficult when scoring defoliation on inaccessible plants high in trees. However, insect herbivory on mistletoe occurs consistently at minor levels on all plants, whereas possum herbivory is obvious, typically occurring as heavier defoliation, and is randomly distributed among plants (Sessions and Kelly 2001b). As a result, it remains possible to attribute coarse defoliation scores to possum herbivory on mistletoe from some distance regardless of insect defoliation. This is because possum herbivory occurs as an obvious effect on top of a constant background level of minor defoliation by insects.

Defoliation scores are not necessarily an indication of plant health. This is because they only record recent browse events. As a result, plants in poor health could record zero defoliation scores even if a plant had lost most of its foliage to earlier herbivory. This is especially so for *P. patulum* which recovers slowly, whereas mistletoe re-growth typically occurs within a year of a browse event (Sessions and Kelly 2001b). This had the potential to obscure the actual condition of plants. To overcome this,

measuring foliage cover of *P. patulum* in combination with defoliation levels, would be a complimentary measure of plant condition.

As discussed above, because most mistletoe plants are high in tree canopies, there is a greater risk of measurement error. For variables with broad parameters, such as foliage cover and defoliation class, adequate assessment of plants could be obtained with the assistance of good binoculars. However, estimating size accurately was problematic. This was made more difficult by a scoring system that requires a three dimensional measurement. Size was considered too unreliable and discarded from the analysis in this study. Unless a sufficient sample of plants can be directly measured, the reliability of size as an indicator of herbivory impact is dubious.

Furthermore, monitoring periods need to be of a sufficient time scale to account for responses and lag effects. Although this study has spanned three year of data, it is still influenced by lag effects as shown by some of the results. Consequently, a longer time frame is required to determine more precisely the trends associated with herbivory. Longer term monitoring will also overcome some of the problems associated with a lack of replication.

Seedling recruitment was not formally measured in this project. Given the importance of recruitment to the conservation of these species, effort should be made to measure this in the future. Thorough searches and recording of new plants in existing sites in conjunction with the current monitoring programme would address this need.

5. Conclusions and recommendations

The presence of *P. patulum* and mistletoe together with a common threat provided a good opportunity to assess the impact of possum herbivory on these species following possum control in the treatment area. The monitoring undertaken as part of this project has shown that possum herbivory was responsible for increasing mortality in *P. patulum* and mistletoe, and impeded growth in *P. patulum*. These results confirm previously anecdotal evidence of these impacts.

There is direct evidence that *P. patulum* is at high risk of extinction from herbivory without intervention. Possums are identified as the major threat to the long term sustainability of *P. patulum* because of the severe impact they have on the mortality of adult plants. With the loss of adult plants, the sustainability of populations is prevented unless juvenile plants can reach maturity. Herbivory on juvenile age classes, however, is likely to impede succession to adulthood.

The pattern of decline observed in northern populations of *P. patulum* is an indication of what to expect in the Ohau catchment if intervention is not forthcoming. In particular, adult plant mortality will increase as possums approach peak densities. Following the loss of adults, a slow decline toward extinction will occur as populations become younger, smaller and less able to recover.

Mistletoe was also shown to be vulnerable to possum herbivory, which is consistent with findings from other research conducted in similar ecosystems. The long-term fate of mistletoe in the presence of ongoing herbivory is less clear. Although mistletoe may suffer a marked reduction in population numbers, including local extinction at some sites, mistletoe's greater environmental plasticity reduces its overall threat to extinction

compared to *P. patulum*. Most likely, mistletoe will persist at inaccessible sites, and/or in 'richer' plant communities, albeit in reduced densities.

Removing possums will significantly reduce the threat to *P. patulum* and mistletoe. Management priorities for *P. patulum* should focus on maintaining and improving the integrity of populations in the Ohau catchment, as these are the best and last representative populations remaining in New Zealand.

Extending the possum control operation from the treatment area to the wider Ohau catchment is recommended. This will have the added benefit of mitigating the threat to mistletoe populations in this area, as well as benefits to the health and function of the wider ecosystem. Northern populations of *P. patulum* require intensive management to prevent extinction in the medium to long term. Consequently, excluding mammalian herbivores from key sites to promote succession of young plants (seedling, saplings and sub-adults) to maturity is recommended.

Management of mistletoe should not be driven by the possibility of national extinction, but rather around maintaining 'desirable densities' of mistletoe in extant populations. This requires an understanding of the inherent role mistletoes have in supporting wider ecosystem function and health, such as relationships with bird species that act as pollinators (Ladley and Kelly 1996). Until there is better understanding of these roles and interactions, maintaining current mistletoe populations and plant densities is desirable. Meeting this objective for the Ohau populations is an inherent part of management recommended for *P. patulum*.

Possum control operations, like that undertaken in the treatment area, provide good opportunities to undertake research on possum impacts on palatable rare species at an ecosystem scale. The approach adopted in this study highlights that measuring appropriate variables in combination with pragmatic study designs ensures key results that are robust to a lack

of replication can be obtained. This approach has wide ranging benefits for conservation managers.

Defoliation levels were important predictors of *P. patulum* and mistletoe survival and growth rates. Consequently, *P. patulum* and mistletoe are potentially good indicator species to judge ecosystem stress from possum herbivory. Managers can undertake field assessments using defoliation scores to gauge impending *P. patulum* (and mistletoe) mortality. This in turn can be used as a guide for when to initiate possum control.

Longer term monitoring of *P. patulum* and mistletoe in the treatment and non-treatment areas will provide greater understanding of possum herbivory on these species. As time progresses, herbivory-related lag effects will fade enabling more confident assessment of trends to be made.

Continuation of the current monitoring is recommended. In addition to the current monitoring regime, assessing foliage cover of *P. patulum* is recommended to provide a more accurate assessment of *P. patulum* condition. Further, recording of new seedlings for both *P. patulum* and mistletoe when they occur in established plots should be incorporated into the current monitoring regime. This will serve as an additional indicator of potential possum impacts on these species over time.

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