

Deer impacts on tawa (*Beilschmiedia tawa*) regeneration

Mark C. Smale

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ABSTRACT

Tawa (*Beilschmiedia tawa*) is the predominant canopy tree species in extensive tracts of old-growth forest across much of the North Island, New Zealand. The regeneration of this slow-growing, late-successional species is crucial for canopy maintenance in these forests. The impacts of herbivory on tawa regeneration were assessed in tawa-dominant forests in the North Island. There was no significant change in seedling densities between 1997 and 2006 in 31 permanent plots at Otamatuna in northern Te Urewera National Park, despite intensive red deer (*Cervus elaphus*) control during this period. Similarly, the exclusion of deer from two larger plots over a similar period in the same area did not affect tawa seedling density. Seedling densities in 15 subplots of large permanent plots elsewhere in the region were not correlated with deer history, which varied from never present to c. 50 years of presence. Seedling populations of thousands per hectare are probably adequate to maintain tawa at current densities; however, populations of hundreds of seedlings per hectare may not be. Established seedling densities in northern Te Urewera National Park were relatively low, ranging from 500 to 1250 per hectare, suggesting there may be cause for concern there. Furthermore, seedling populations declined by 16%–82% over 22–40 years in four of the permanent subplots. Although the data analysed here did not implicate deer herbivory in these declines, previous exclusion studies over longer periods in the same region did. The overall impression from the equivocal results reviewed here is that herbivory may be impairing tawa regeneration in some places. Recommendations are made for further research requirements.

Keywords: *Beilschmiedia tawa*, herbivory, deer, *Cervus elaphus*, regeneration, New Zealand

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1. Introduction

Tawa (*Beilschmiedia tawa*) is the predominant canopy tree species in extensive tracts of old-growth forest across much of the North Island, New Zealand, contributing up to two-thirds or more of the basal area (and therefore much of the biomass) in 'tawa-dominant' forests (unpubl. data). It is, therefore, a 'keystone' species and its regenerative health is crucial for canopy maintenance in these forests. Although introduced deer (mostly red deer *Cervus elaphus*) have now been present for many decades in most tawa-dominant forests and introduced possums (*Trichosurus vulpecula*) have been present in them all, tawa has not been a species of concern for managers or researchers. However, staff of the Department of Conservation (DOC) have recently become concerned that herbivory by introduced mammals may be affecting the regenerative health of this species (C. Ward, DOC, pers. comm.)

2. Objectives

The five main objectives were to:

- Review the ecology of tawa in tawa-dominant forests
- Assess the impacts of herbivory by deer on the regeneration of tawa in tawa-dominant forests in the North Island
- Review other biotic and abiotic factors that may affect tawa regeneration
- Suggest quantitative criteria that are indicative of 'adequate tawa regeneration'
- Make recommendations for further research

3. Methods

3.1 ECOLOGY OF TAWA IN TAWA-DOMINANT FORESTS

The regenerative ecology of tawa in tawa-dominant forests was reviewed from existing literature.

3.2 DEER IMPACTS ON TAWA REGENERATION

3.2.1 Permanent plots in Otamatuna Management Area

In 1997, 40 permanent 9 m × 9 m (0.0081 ha) plots were established within the Otamatuna Management Area of Te Urewera National Park (Bockett 1998), a 2500-ha area in the lower Tauranga River catchment. This area mostly comprises unlogged tawa-dominant forest, which ranges in elevation from 160 m to 720 m a.s.l. and has been subject to intensive pest (including herbivore) control since 1996 (Shaw et al. 1996). Plots were established under mature tawa canopies at between 180 m and 600 m a.s.l., with ten plots located on each of four landforms:

- North-facing hillslopes at higher elevation (480–600 m a.s.l.)
- South-facing hillslopes at higher elevation
- Hillslopes at lower elevation (180–300 m a.s.l.)
- Terraces at lower elevation

Within each plot, seedling densities were recorded in five height classes (< 15 cm, 15–45 cm, 45–75 cm, 75–105 cm and 105–145 cm) in 25 systematically located but unmarked 1 m × 1 m 0.0001-ha subplots.

In 2006, the 31 plots that could be relocated were re-sampled. Because seedling subplots were not permanently marked, repeated measures could only be assumed for each whole plot, rather than individual subplots. A general linear model (GLM) with a negative binomial error structure was used to test whether the total density of tawa seedlings and the density in each of the five height classes varied between the two surveys (1997 v. 2006) and between landforms (terraces v. steep slopes v. north-facing slopes v. south-facing slopes).

3.2.2 Exclosure plots in Otamatuna Management Area

In 1998, two standard 20 m × 20 m (0.04 ha) deer-exclosure plots (Allen 1993) with paired controls were established at Pohatuatua and Mapou in the Otamatuna Management Area. Within each plot, seedling densities were recorded in five height classes (< 15 cm, 15–45 cm, 45–75 cm, 75–105 cm and 105–135 cm) in 24 0.49-m radius 0.000075-ha subplots. Data for the smallest height class (< 15 cm) were collected as frequencies.

In 2006, both pairs of plots were re-sampled and data analysed with paired *t*-tests. Feral pigs (*Sus scrofa*) had breached the Mapou exclosure and interfered with seedling subplot markers, so that seedling subplots could not be relocated with sufficient accuracy within it and the control to be treated as repeated measures.

3.2.3 Long-term data from Ecological Transects

Densities of established tawa seedlings (> 15 cm tall and < 2.5 cm diameter at breast height (DBH)) were examined in 15 permanent 210 m × 20 m (0.4 ha) plots ('Ecological Transects') in tawa-dominant forest across a wide area of the middle North Island. Transects were established from 1957 to 1962 to monitor long-term forest dynamics and were deliberately placed across the 'grain' of the landscape to capture the range of microtopographic variation present (McKelvey et al. 1958). They covered a range of deer occupation histories, from 0 (i.e. absent) to nearly 50 years at time of plot establishment. Within each plot, seedling subplots comprised 96 contiguous 2 m × 2 m subplots (total area 0.0384 ha) running almost the entire length of the larger 210-m-long plot.

The relationship between initial tawa seedling densities and deer occupation history (categorised as absent/brief and prolonged) at the time of plot establishment was tested by ANOVA. For four transects, time-series data were also available, allowing changes over 22–40 years to be examined.

4. Results

4.1 ECOLOGY OF TAWA IN TAWA-DOMINANT FORESTS

4.1.1 Importance

Tawa is the predominant canopy tree species in extensive tracts of old-growth forest in a wide swathe across the middle of the North Island (J.L. Nicholls, cited in Knowles & Beveridge 1982). As a classic slow-growing, shade-tolerant, late-successional species (Smale et al. 1986), it is absent from the earlier phases of successional seres. Tawa is an important component of four major forest classes (J.L. Nicholls, cited in Knowles & Beveridge 1982), two of which are found in the northern North Island (kauri (*Agathis australis*)-podocarp/hardwoods, and podocarp/taraire (*Beilschmiedia tarairi*)-tawa), and two of which are in the middle North Island (rimu (*Dacrydium cupressinum*)/tawa, and podocarp/tawa-beech (*Nothofagus* spp.)). However, its population structure, dynamics and successional status in each of these remains to be adequately studied. Rimu/tawa is the classic 'tawa-dominant' forest class and, along with logged variants, is the most common of these associations. Tawa is also prominent in one type, podocarp/tawa, which falls within another forest class, rimu-matai (*Prumnopitys taxifolia*)-general hardwoods.

In many forests, the importance of tawa is increasing in response to both natural (e.g. the demise of conifer cohorts in successional forests) and human-induced (e.g. selective harvesting of conifers, and the decline of other more palatable species such as kamahi *Weinmannia racemosa*) changes (unpubl. data; Smale & Beveridge 2007). In c. 1960, tawa contributed an average of 53% to the basal area of six Ecological Transects in rimu/tawa forest; this had risen to 60% some 40 years later (unpubl. data).

4.1.2 Regeneration strategy

Tawa fruits annually, but seed crops vary considerably in quantity, with mast years occurring approximately every 7 years (Knowles & Beveridge 1982). Seed has no dormancy mechanism and loses viability if desiccated (Knowles & Beveridge 1982). In most tawa-dominant forests, tawa populations appear to be unevenly aged and undergoing continuous replacement by individuals or small groups (Smale et al. 1986). Seedlings (< 145 cm tall) are slowly incorporated into long-lived, slow-growing banks of persistent 'advance growth' (large seedlings and small saplings, > 145 cm tall and < 5 cm DBH; West 1995). They can develop to maturity, albeit very slowly, under existing canopies of tawa or other species (Smale & Kimberley 1983), but growth rates are considerably enhanced by increased illumination (Smale & Kimberley 1986). In seedlings (< 2.5 cm DBH), average height growth rates range from 3 cm/year in dominated individuals (i.e. those that are overtopped by other vegetation) to 12 cm/year in plants with full overhead light (Smale & Kimberley 1986). In saplings (2.5–10 cm DBH), average diameter growth rates range from 1 mm/year in dominated individuals to 2–3 mm/year with full light (Smale & Kimberley 1986). In canopy trees, average diameter growth rates vary widely between localities, ranging from 0.5 mm/year to 2.6 mm/year (Smale et al. 1986). The influence of root competition remains unknown.

Because of its relatively minor importance as a timber species and its often conspicuous regeneration, the factors controlling regeneration patterns in tawa have received less attention than those of conifers. A recent study in tawa-dominant forest in the Urewera region (Carswell et al. 2007) indicated that regeneration occurs in response to a suite of coinciding environmental factors (high tawa density in the canopy, high nitrogen levels in the soil, and lack of disturbance) rather than any single factor. This may help to explain the patchiness that seems to be a common feature of tawa regeneration.

Seedlings, saplings and even trees can prolong their existence by vegetative regrowth after dieback. Suppressed seedlings can persist for many decades, perhaps even a century or more, without discernible growth; for example, heavily shaded c. 70-cm-tall seedlings in tawa-dominant forest on the Mamaku Plateau did not grow discernibly in height for 26 years (unpubl. data). These periods of suppression cannot necessarily be detected from growth rings, as a suppressed tree in a permanent plot in Rotoehu Forest that had not grown perceptibly for 25 years did not form normal growth rings over that period (unpubl. data). Accurate ageing by growth ring analysis is, therefore, problematic. This problem is exacerbated by the capacity of seedlings to undergo repeated vegetative regrowth after dieback. Nevertheless, maximum lifespans of trees that have not endured long periods of suppression in the understorey are probably in the order of 450 years (West 1986, cited in West 1995).

4.1.3 Canopy replacement mechanisms

Canopy replacement mechanisms in tawa-dominant forest have received little attention. In the only quantitative study to date, in Rotoehu Forest, ‘reciprocal replacement’ was evident, with tawa replacing kohekohe (*Dysoxylum spectabile*) more commonly than itself, and vice versa (Smale & Kimberley 1983). Reciprocal replacement mechanisms like this may help to explain the apparent paucity in places of tawa regenerating under itself. Esler (1967) previously suggested that the same phenomenon occurred on Kapiti Island. Tawa also commonly replaces emergent conifers *in situ*, with tawa ‘advance growth’ developing beneath senescent podocarps (Beveridge 1973; Smale et al. 1987).

4.2 DEER IMPACTS ON TAWA REGENERATION

4.2.1 Permanent plots in Otamatuna Management Area

Densities of ephemeral seedlings (< 15 cm tall) ranged from 0 to 6400 seedlings per hectare (averaging 1006/ha) in 1997 and from 0 to 8000 seedlings per hectare (averaging 1394/ha) in 2006. Total densities of established seedlings (> 15 cm tall) ranged from 0 to 1240 seedlings per hectare (averaging 108/ha) in 1997 and from 0 to 1160 seedlings per hectare (averaging 105/ha) in 2006. The total density of tawa seedlings and the density in each of the five height classes did not vary significantly (GLM with negative binomial structure) between landforms (terraces v. steep slopes v. north-facing slopes v. south-facing slopes) within measurement years, and did not change between the two surveys (1997 v. 2006) (Table 1). Height frequency distributions changed little over the 9-year period.

TABLE 1. TAWA (*Beilschmiedia tawa*) SEEDLING DENSITIES IN 31 PERMANENT 0.0081-ha PLOTS IN TAWA-DOMINANT FOREST IN OTAMATUNA MANAGEMENT AREA, TE UREWERA NATIONAL PARK.

Seedlings are separated into five height classes. Densities (number of seedlings per hectare) were measured in 1997 and 2006. None of the differences between landforms within years or between years within landforms were significant at $P < 0.05$.

LANDFORM	< 15 cm		15-45 cm		45-75 cm		75-105 cm		105-145 cm		TOTAL	
	1997	2006	1997	2006	1997	2006	1997	2006	1997	2006	1997	2006
N-facing ($n=8$)	750	1400	400	300	400	200	150	250	0	100	1700	2250
S-facing ($n=9$)	356	622	444	489	356	444	267	178	178	44	1601	1778
Hillslope ($n=7$)	1200	857	400	286	114	171	0	57	0	57	1714	1429
Terrace ($n=7$)	1943	2914	400	457	171	171	57	57	0	0	2571	3600
Mean ($n=31$) (\pm SEM)	1006 (\pm 293)	1394 (\pm 328)	413 (\pm 84)	387 (\pm 86)	271 (\pm 73)	258 (\pm 71)	129 (\pm 50)	142 (\pm 54)	52 (\pm 31)	52 (\pm 25)	1858 (\pm 349)	2232 (\pm 399)

4.2.2 Exclosure plots in Otamatuna Management Area

Total tawa seedling densities did not change significantly between 1998 and 2006 in the control plot (paired *t*-test, $t = -2.0$, $df = 23$, $P < 0.06$) or the exclosure (paired *t*-test, $t = -1.0$, $df = 23$, $P < 0.3$) at Pohatuatua (Table 2). At Mapou, seedling densities scarcely changed in either control or exclosure.

TABLE 2. TAWA (*Beilschmiedia tawa*) SEEDLING DENSITIES IN TWO 0.04-ha EXCLOSURES AND THEIR ASSOCIATED CONTROL PLOTS IN TAWA-DOMINANT FOREST IN THE OTAMATUNA MANAGEMENT AREA, TE UREWERA NATIONAL PARK.

Densities (number of seedlings per hectare) were measured in 1998 and 2006. Percentages for seedlings < 15 cm tall are frequencies of occurrence in 24 0.0005-ha subplots.

SITE	EXCLOSURE						CONTROL					
	< 15 cm		15-45 cm		46-135 cm		< 15 cm		15-45 cm		46-135 cm	
	1998	2006	1998	2006	1998	2006	1998	2006	1998	2006	1998	2006
Pohatuatua	25%	21%	0	0	0	83	46%	79%	250	2250	167	83
Mapou	21%	46%	333	250	333	83	17%	8%	250	250	667	750

4.2.3 Other exclosure plots in Te Urewera National Park

In lowland forest at a variety of locations in Te Urewera National Park, the frequency of small tawa seedlings (15-140 cm tall) after 12-20 years was significantly ($P < 0.05$) higher inside the 14 exclosures (15%) where the species was present than in the associated control plots (6%) outside them (Allen et al. 1984). The frequency of ephemeral seedlings (< 15 cm tall) did not differ between exclosures and controls, however.

4.2.4 Long-term data from Ecological Transects

In the Ecological Transects, seedling populations of tawa at the time of plot establishment (1957-1962) varied by two orders of magnitude, from c. 400 stems/ha to over 31 000 stems/ha (Table 3). Densities of small (15-140 cm tall) and large (> 140 cm tall and < 2.5 cm DBH) seedlings were very strongly correlated with each other ($r = 0.99$, $P < 0.01$). However, seedling densities were not correlated with deer occupation history (for small seedlings $F = 0.1$, $df = 1, 14$, $P < 0.81$; for large seedlings $F = 0.21$, $df = 1, 14$, $P < 0.65$; for total seedlings $F = 0.01$, $df = 1, 14$, $P < 0.91$). In all four Ecological Transects for which time-series seedling data were available, seedling populations of tawa decreased markedly over periods of 22-40 years (Table 4). Decreases of all seedlings ranged from 16% to 82%, and averaged 52%. The decrease in small seedling densities ranged from 6% to 81%, averaging 50%, and the decrease in large seedling densities ranged from 17% to 90%, averaging 59% (Table 4).

TABLE 3. ORIGINAL TAWA (*Beilschmiedia tawa*) SEEDLING DENSITIES IN 15 0.0384-ha ECOLOGICAL TRANSECTS IN TAWA-DOMINANT FORESTS IN 12 LOCALITIES IN THE MIDDLE NORTH ISLAND.

Deer = number of years deer have occupied the area at the time of plot establishment. Small seedlings: 15–140 cm tall; large seedlings: > 140 cm tall and < 2.5 cm DBH.

TRANSECT	LOCALITY	ESTABLISHED	FOREST CLASS	DEER (y)	SEEDLING DENSITY (STEMS/ha)		
					SMALL	LARGE	TOTAL
1*	Mamaku	1959	Rimu/tawa	0	3515	469	3984
6*	Whirinaki	1957	Podocarp/tawa	27	14244	1875	16119
7.2*	Whirinaki	1957	Podocarp/tawa	22	10495	572	11067
15	Rotoma	1959	Rimu/tawa	38	781	26	807
17	Kaimai†	1960	Rimu/tawa	0	417	130	547
18	Kaimai‡	1960	Tawa (crown-fired rimu/tawa)	0	859	651	1510
23	Pureora	1959	Podocarp/tawa	0	25104	6484	31588
24	Pureora	1959	Podocarp/tawa	0	6432	182	6614
27	Ikawhenua	1960	Podocarp/hardwoods	45	3203	781	3984
36	Mamaku	1960	Rimu/tawa	0	2083	391	2474
41	Mangorewa	1962	Rimu/tawa	0	1693	469	2162
42	Ikawhenua	1962	Podocarp/hardwoods	47	5885	1068	6953
44*	Waioeka	1962	Rimu/tawa	5	3151	1250	4401
45	Waioeka	1962	Rimu/tawa	5	860	156	1016
54	Urewera	1963	Rimu/tawa	13	365	52	417

* Transect with re-sampled seedling plots.

† Feral cattle (*Bos taurus*) were probably present at time of plot establishment.

‡ Feral cattle were present at time of plot establishment.

TABLE 4. CHANGES IN TAWA (*Beilschmiedia tawa*) SEEDLING DENSITIES IN FOUR 0.0384-ha ECOLOGICAL TRANSECTS IN TAWA-DOMINANT FORESTS IN THREE LOCALITIES IN THE MIDDLE NORTH ISLAND OVER 22–40 YEARS.

Remeasurement period (years) presented in parentheses alongside each locality. Deer = number of years deer have occupied the area at the time of plot establishment. Small seedlings: 15–140 cm tall; large seedlings: > 140 cm tall and < 2.5 cm DBH.

TRANSECT	LOCALITY	DEER (y)	SEEDLING DENSITY (STEMS/ha)								
			SMALL			LARGE			TOTAL		
			START	END	CHANGE	START	END	CHANGE	START	END	CHANGE
1	Mamaku (40)	0	3515	2109	-40%	469	390	-17%	3984	2499	-37%
6	Whirinaki (25)	27	14244	2708	-81%	1875	183	-90%	16119	2891	-82%
7.2	Whirinaki (24)	22	10495	2838	-73%	572	78	-86%	11067	2916	-74%
44	Waioeka* (22)	5	3151	2969	-6%	1250	729	-42%	4401	3698	-16%

* A small number of feral goats (*Capra hircus*) was present in the vicinity at the time of plot establishment and for c. 15 years afterwards.

4.3 ADDITIONAL FACTORS THAT MAY AFFECT TAWA REGENERATION

4.3.1 Biotic factors

Through the many decades of concern about and research into the impacts of introduced deer on native forests, tawa has not been a species of interest for managers or researchers. This is because it is generally regarded as relatively unpalatable to deer over most of its range. However, heavy browsing on seedlings and small saplings has been recorded in parts of the Urewera region (G.T. Jane, cited in Knowles & Beveridge 1982). Young coppice shoots appear to be particularly palatable (Knowles & Beveridge 1982). Hedged seedlings—evidence of sustained earlier browsing—were widely observed at Otamatuna in the present study. However, the remarkable persistence of tawa and its capacity for vegetative regrowth limits the impacts of deer and other mammals on it, because at least some damaged plants can regrow following browsing.

Across most of its range, tawa foliage is generally regarded as relatively unpalatable to possums (*Trichosurus vulpecula*), although it is a significant component of possum diet in the southern North Island where it is a very minor canopy component (Brockie 1992). Feral cattle (*Bos taurus*) and feral goats (*Capra hircus*), both of which were present at the time of plot establishment in at least two of the Ecological Transects, may browse tawa seedlings, although published evidence is lacking.

Introduced mammals may be causing reduced recruitment, either directly or indirectly, at one or more stages of the regeneration cycle (see Allen et al. 2002):

- Flower pollination: As with much of the New Zealand flora, pollination agents for tawa are poorly known, but probably include insects and wind. Pollination failure seems unlikely to be linked to reduced regeneration.
- Fruitfall: Possums consume unripe fruit on the tree (Knowles & Beveridge 1982), but the significance of this is unknown. Reduced fruitfall may be a factor involved in reduced regeneration.
- Fruit dispersal: The only known animal disperser of tawa fruit is the New Zealand pigeon (*Hemiphaga novaeseelandiae*), which has declined greatly over most of its range because of predation by introduced mammals (Clout et al. 1995). The significance of this reduction for tawa dispersal is unknown. Dispersal is presumably less important within old-growth tawa-dominant forest than in colonising seral forests, where longer distance dispersal is required; however, reduced dispersal may still contribute to reduced regeneration.
- Seed predation after fruitfall or dispersal: Possums and feral pigs eat ripe fruit after it has fallen (Knowles & Beveridge 1982), but the fate of the seeds that are ingested and the significance of mammalian predation are unknown. Larvae of a native moth, *Cryptaspasma querula*, also consume fallen fruit, destroying the seed, sometimes in large quantities (Knowles & Beveridge 1982). Seed predation may be a factor contributing to reduced regeneration.
- Seed germination: Understoreys that have been depleted by herbivory may be expected to have generally lower humidity than intact ones, although this

has not been demonstrated. Since tawa seed quickly loses viability if it dries out (Knowles & Beveridge 1982), reduced germination may contribute to reduced regeneration.

- Seedling establishment and survival: Seedlings are browsed by deer under some circumstances (Knowles & Beveridge 1982). In addition, like seeds, seedlings are also susceptible to damage (and death) from climatic extremes, including drought (Knowles & Beveridge 1982), as may be experienced in understoreys that have been depleted by herbivory. Reduced seedling survival as a result of microclimatic conditions that have been altered by herbivory may contribute to reduced regeneration, although this is probably less important in old-growth forest than in isolated forest fragments.

4.3.2 Abiotic factors

As a typical rainforest species, tawa is sensitive to wind exposure, drought, snow and frost, especially unseasonal frost (Knowles & Beveridge 1982; Kelly 1987). As mentioned in section 4.3.1, abiotic factors (microclimate) may be impairing regeneration success at one or more stages of the regeneration cycle through their interaction with biotic factors (herbivory). Climatic change, e.g. an increased frequency of frost or drought, could also be involved.

5. Discussion

5.1 DEER IMPACTS ON TAWA REGENERATION

Red deer are likely to have been present at Otamatuna for at least 50 years, and possibly as long as 70 years (McKelvey 1973). There are at least two possible explanations for the lack of change in tawa seedling populations after a decade of intensive deer control at this site:

1. Deer have had little effect (either direct or indirect) on tawa seedling densities at Otamatuna, so a marked reduction in the deer population—and thus browsing pressure—in the area is unlikely to have made any substantial difference to the tawa seedling population.
2. Deer have substantially reduced tawa seedling densities directly and/or indirectly, but the deer population in the area has not been sufficiently reduced for long enough to allow recovery to occur within the assessment period.

The lack of correlation between seedling densities and deer occupation history suggests that any link between deer herbivory and tawa seedling density may be weak, and that other factors may also be involved. Variation in seedling densities among the Ecological Transects seems unlikely to represent microsite (e.g. ridge crest v. valley floor) variation, because the transects were so large and were placed to capture much of the range of microtopographic variation in the landscape; therefore, other factors must be responsible.

The regenerative health of tawa in tawa-dominant forest is a critical issue because of the widespread occurrence of these forests and the increasing importance of tawa in many of them. Established seedling (> 15 cm tall) densities in northern Te Urewera National Park were relatively low, ranging from 0 to 1240 seedlings per hectare. This is within the lower range for the Ecological Transects, which are dispersed across a much wider area (see section 4.2.5), suggesting that there may be cause for concern. Herbivory can alter forest composition in both direct and indirect ways: as well as the direct effects of species-specific herbivory, changes in plant abundance can occur indirectly as a result of interspecific competitive effects. This means that although a species like tawa may be relatively unpalatable, herbivory-induced shifts in the composition of canopies and/or understoreys may reduce its population, e.g. through altered understorey microclimate or through increased competition with enlarged populations of other relatively unpalatable species.

Major declines in established seedling populations over substantial periods of time in widely disparate localities are not expected, and are cause for concern in a species like tawa that has a continuous replacement strategy. Reduced recruitment may be occurring at one or more stages of the regeneration cycle: pollination, fruitfall, fruit dispersal, seed predation after fruitfall or dispersal, germination, seedling establishment, and/or survival. The time-series data analysed in this study did not support the notion that deer herbivory is affecting the regenerative health of tawa in tawa-dominant forests in the middle North Island. However, earlier exclosure studies over longer periods of time and a much wider area of Te Urewera National Park (Allen et al. 1984) did suggest a negative impact of deer herbivory on tawa regeneration. Thus, it would be unwise to definitively exclude herbivory as a factor in tawa regeneration decline on the basis of the limited data available to date. The overall, if weak, impression from the equivocal results reviewed here is that herbivory may be impairing tawa regeneration in some places but not others.

Since tawa is a slow-growing, long-lived species, there is likely to be a considerable delay before any reduction in the regenerative phase of its life cycle becomes apparent in canopy replacement. Thus, still plentiful understorey sapling and subcanopy small tree populations may be giving a false impression of the regenerative health and future state of the canopy in many tawa-dominant forests.

5.2 QUANTITATIVE CRITERIA INDICATIVE OF 'ADEQUATE TAWA REGENERATION'

The concept of 'adequate tawa regeneration' implies the maintenance of tawa populations at their current densities. The dynamic nature of some forests in which tawa is prominent makes this problematic. For example, the density of tawa trees (> 30 cm DBH) in the canopy increased by an average of nearly 30 trees/ha (31%) over c. 40 years between c. 1960 and c. 2000 in most Ecological Transects in the rimu-matai-general hardwoods forest, but decreased by an average of nearly 7 trees/ha (6%) in most transects in rimu/tawa forest. The densities of saplings/small trees (2.5–30 cm DBH) decreased by an average of 233 stems/ha (28%) in almost all plots in the rimu-matai-general hardwoods forest, but showed no

consistent pattern of change in the rimu/tawa forest (unpubl. data). This shows that, assuming that herbivory has not substantially affected plants with larger stem sizes, the rimu-matai-general hardwoods class of forest appears to be inherently unstable and currently undergoing a shift toward greater tawa dominance in the canopy and lesser tawa prominence in the understorey. In contrast, the rimu/tawa class appears to be relatively stable. Therefore, the concept of 'adequate tawa regeneration' may not apply to apparently successional forest types, such as the widespread podocarp/tawa type (which is part of the rimu-matai-general hardwoods class) of the Volcanic Plateau and neighbouring regions, in which tawa populations are currently unstable.

The densities of tawa of all sizes are highly variable. Initial densities of established tawa seedling populations (> 15 cm tall and < 2.5 cm DBH) in the Ecological Transects in tawa-dominant forest sampled here varied by two orders of magnitude, from c. 400 stems/ha to over 31 000 stems/ha. Sapling/small tree (2.5–30 cm DBH) densities also varied by an order of magnitude (60–1400 per hectare). Tree (> 30 cm DBH) densities were more consistent, varying from 80 to 200 trees per hectare. These population structures suggest that mortality occurs throughout the life-stages of tawa, but at a diminishing rate; mortality rates are highest in ephemeral seedlings, lower in established seedlings, and lower still in saplings and small trees. Given the fact that not all seedlings survive to become saplings and trees, larger populations of seedlings are required than saplings or trees to maintain current tree populations. In other words, to sustain existing sapling, small tree and tree densities, seedling densities will need to exceed those of the next size-class, i.e. saplings and small trees (60–1400 stems/ha).

6. Recommendations

6.1 DEER HERBIVORY AND TAWA REGENERATION

To gain a better understanding of the impacts of herbivory by deer on the regeneration of tawa in tawa-dominant forests in the North Island, several steps should be taken:

- The 31 permanent plots and the two exclosures with paired controls in the Otamatuna Management Area of Te Urewera National Park should be maintained and re-sampled to see whether seedling populations respond to a greatly reduced deer population.
- Other intact exclosure plots in forest in the wider Te Urewera National Park in which tawa is an important component should be re-sampled to help elucidate the impacts of deer herbivory on tawa regeneration and substantiate the earlier conclusions of Allen et al. (1984).
- A review and meta-analysis of exclosure plot data from tawa-dominant forests elsewhere in the North Island should be conducted to help clarify the impacts of deer herbivory on tawa regeneration.

- Some or all of the seedling subplots in the 15 longer term Ecological Transects should be re-sampled to ascertain the regenerative health of tawa over a wider area, to help determine the geographic extent of declining seedling populations and to help elucidate the possible role of deer herbivory in this decline.
- Canopy replacement mechanisms in forest in which deer are sparse or absent should be investigated, to shed light on whether the apparent patchiness of tawa regeneration is a natural or herbivory-induced phenomenon.
- Plots should be established in forests without deer, to provide controls against which to measure deer impacts.

6.2 CRITERIA FOR 'ADEQUATE TAWA REGENERATION'

In order to suggest criteria for 'adequate tawa regeneration', we first need to gain a better understanding of the population dynamics of tawa populations at all stages of the life cycle. To scale these criteria up to the landscape level, demographic data on both recruitment and mortality rates need to be collected along gradients of deer management (excluded, moderate control and uncontrolled) and soil fertility across a spectrum of the major forest classes in which tawa is important. This information can only be gained by repeated measures of individually tagged stems. At present, such data are only available for larger stems (> 30 cm) in the Ecological Transects. Therefore, the following additional research is recommended:

- Transects that have been monitored since 1999 should be re-sampled to obtain data on small and large tree (> 10 cm DBH) dynamics.
- Transects that have been monitored since 2006 should be re-sampled to obtain data on sapling, small tree and large tree (> 2.5 cm DBH) dynamics.
- Some seedling populations should also be tagged and monitored over time, to assess recruitment and mortality rates in them. Currently, tawa in Ecological Transects are being tagged down to 2.5 cm DBH, which includes saplings but not seedlings; thus, seedling population dynamics are still being overlooked.

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8. References

- Allen, R.B. 1993: A permanent plot method for indigenous forests. Manaaki Whenua Press, Lincoln. 35 p.
- Allen, R.B.; Payton, I.J.; Knowlton, J.E. 1984: Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures. *New Zealand Journal of Ecology* 7: 119-130.
- Allen, R.B.; Rogers, G.M.; Stewart, G.H. 2002: Maintenance of key tree species. *Science for Conservation* 190. Department of Conservation, Wellington. 60 p.
- Beveridge, A.E. 1973: Regeneration of podocarps in a central North Island forest. *New Zealand Journal of Forestry* 18: 23-35.
- Bockett, F.K. 1998: The impacts of ungulates on podocarp/tawa forest, northern Te Urewera National Park. Unpublished MEnvSc thesis, University of Auckland, Auckland. 146 p.
- Brockie, R. 1992: A living New Zealand forest. David Bateman, Auckland. 172 p.
- Carswell, F.E.; Richardson, S.J.; Doherty, J.E.; Allen, R.B.; Wisser, S.M. 2007: Where do conifers regenerate after selective harvest? A case study from a New Zealand conifer-angiosperm forest. *Forest Ecology and Management* 253: 128-147.
- Clout, M.N.; Pierce, R.J.; Robertson, H.A. 1995: Breeding and survival of New Zealand pigeons *Hemiphaga novaeseelandiae*. *Ibis* 137: 246-271.
- Esler, A.E. 1967: Vegetation of Kapiti Island. *New Zealand Journal of Botany* 5: 353-393.
- Kelly, D. 1987: Slow recovery of *Beilschmiedia tawa* after severe frosts in inland Taranaki. *New Zealand Journal of Ecology* 10: 137-140.
- Knowles, F.B.; Beveridge, A.E. 1982: Biological flora of New Zealand 9. *Beilschmiedia tawa* (A. Cunn.) Benth. et Hook. f. ex Kirk (Lauraceae). Tawa. *New Zealand Journal of Botany* 20: 37-54.
- McKelvey, P.J. 1973: The pattern of the Urewera forests. *Technical Paper No. 59*. Forest Research Institute, New Zealand Forest Service. 127 p.
- McKelvey, P.J.; Cameron, R.J.; Warren, A.D. 1958: Design for a forest study. *New Zealand Journal of Forestry* 7: 116-122.
- Shaw, W.B.; Shaw, P.G.; Gooch, L. 1996: Northern Te Urewera ecosystem restoration strategy, a mainland ecosystem restoration project. Wildlands Consultants Contract Report 154 to Department of Conservation (unpublished).
- Smale, M.C.; Bathgate, J.L.; Guest, R. 1986: Current prospects for tawa. *New Zealand Journal of Forestry* 31: 13-18.
- Smale, M.C.; Beveridge, A.E. 2007: Long-term impacts of selective harvesting on a New Zealand conifer-hardwood forest. *New Zealand Journal of Forestry Science* 37: 3-22.
- Smale, M.C.; Beveridge, A.E.; Pardy, G.F.; Steward, G.A. 1987: Selective logging in podocarp/tawa forest at Pureora and Whirinaki. *New Zealand Journal of Forestry Science* 17: 29-50.
- Smale, M.C.; Kimberley, M.O. 1983: Regeneration patterns in *Beilschmiedia tawa*-dominant forest at Rotoehu. *New Zealand Journal of Forestry Science* 13: 58-71.
- Smale, M.C.; Kimberley, M.O. 1986: Growth of naturally regenerated *Beilschmiedia tawa* and podocarps in unlogged and selectively logged podocarp/tawa forest, Pureora. *New Zealand Journal of Forestry Science* 16: 131-141.
- West, C.J. 1995: Sustainability of *Beilschmiedia tawa*-dominated forest in New Zealand: population predictions based on transition matrix model analysis. *Australian Journal of Botany* 45: 51-71.

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