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EFFECTS OF UNGULATES ON STRUCTURE AND SPECIES COMPOSITION IN THE UREWERA FORESTS AS SHOWN BY EXCLOSURES

Summary: Seventeen exclosures were built by the New Zealand Forest Service within Urewera forests over the period 1961-68 to exclude ungulates. Forest structure and species composition inside and outside these exclosures were compared in 1980-81. Some relatively shade tolerant species such as the fern *Asplenium bulbiferum,* the liane *Ripogonum scandens,* the sub-canopy shrubs *Geniostoma ligustrifolium* and *Coprosma australis* and the canopy species *Beilschmiedia tawa* were less abundant in certain tiers outside the exclosures than inside. By contrast, only a few species were more abundant outside then inside the exclosures. These included the unpalatable shrub *Pseudowintera colorata,* turf-forming *Uncinia* species and *Cardamine debilis*. Overall density and species richness for small diametered trees and for the sapling tier were lower outside the exclosures than inside. Despite the large reduction in ungulate numbers throughout Urewera forests these introduced browsing animals, particularly deer, still affect the structure and composition of most forest types.

Keywords: regeneration; forest; introduced animals; ungulates; deer, Cervus sp., Cervidae; exclosure; Urewera; New Zealand.

Introduction

The Urewera forests cover about 400 000 ha of steep highlands, of which approximately half lie within Urewera National Park (McKelvey, 1973). In the more northern and eastern parts, the distribution of the dominant canopy species is related to altitude (McKelvey, 1973). There is a transition from conifer/mixed hardwood forest on the lowlands to conifer/mixed hardwood/beech and conifer/beech at middle altitudes and pure beech forest on the upper slopes (McKelvey, 1973). This transition forms a continuum in terms of changing species composition with increasing altitude. The more widely distributed, physiognomically dominant canopy species include the conifers rimu *(Dacrydium cupressinum*[3]*)* and miro *(Podocarpus ferrugineus),* the hardwoods kama hi (W*einmannia racemosa),* tawa *(Beilschmiedia tawa),* rewarewa *(Knightia excelsa),* rata *(Metrosideros robusta)* and *Laurelia novae-zelandiae,* and the beech species red *(Nothofagus fusca)* and silver *(N. menziesii)* beech. Differences occur in forest composition on different sites at the same altitude. On recently disturbed areas, for example, landslides or burns, seral forests of lower stature have developed. Important canopy species here include mahoe *(Melicytus ramiflorus), Leptospermum ericoides, Fuchsia excorticata,* pate *(Schefflera digitata),* putaputaweta *(Carpodetus serratus),* and *Pseudopanax arboreus*[4]. In the south-west, however, apparently anomolous species distributions, not fully adjusted to altitude, have been explained in terms of recent volcanic activity (McKelvey, 1973). Various other factors have left an imprint on the vegetation. Grant (1963) proposed that the forests of the Huiarau Range (Fig. 1) were severely damaged on an extensive scale, about 1650 A.D., probably by exceptional winds. Human activities have influenced the Urewera forests for nearly 1000 years; extensive areas in the lower altitude forests were burnt by the early Maoris (McKelvey, 1973). More recently, introduced browsing animals have established, and their impact on the forests has been described in a number of papers (McKelvey, 1959; James and Wallis, 1969; Wallis and James, 1972; McKelvey, 1973) and numerous unpublished New Zealand Forest Service (NZFS) reports. The liberation and spread of introduced animals in the Urewera forests has been documented by McKelvey (1973) and J. E. Knowlton (1982, unpublished NZFS report).

Over the period 1961-68 NZFS established 17 fenced exclosures, 15 within Urewera National Park, to determine the effects of fencing out introduced ungulates. They were constructed of a fine wire mesh, from ground level to approximately 2 m in height, supported by iron standards at the corners and along the sides (see Fig. 3). The exclosures were located in stands with high ungulate usage, e.g., intensive browse and trampling. Although these exclosures covered a range of forest types and sites (Fig. 1, Appendix 1), they were not representative of the Urewera

[3]. Plant nomenclature follows Allan (1961) and Moore and Edgar (1970) unless otherwise stated.
[4]. for *Pseudopanax* spp. nomenclature see Table 1.

area as a whole but were concentrated in the 300-400 m altitudinal band, with 12 exclosures located on slopes of less than 20°. The Urewera Ranges are described as steep-sloped (30° to 50°) mountain ranges (Wallis and James, 1972) which have an altitudinal range from 182 m asl to 1436 m (McKelvey, 1973). The exclosure sites lie within the more northern and eastern forests (Fig. 1).

Parent rocks are mainly Mesozoic greywacke and argillite, with areas of Cenozoic sandstone and siltstone on the eastern fringe of the Urewera (N.Z. Geological Survey, 1972). The soils are largely sandy silts and sands which have developed on rhyolitic ash (N.Z. Soil Bureau, 1954), with skeletal soils on steeper slopes. Recent ash depositions in this area are documented by Pullar and Birrell (1973). Mean annual rainfall ranges from 1524 mm in the north-west to 3175 mm in the south-east, the gradient being modified by topography (Wallis and James, 1972).

The density and combination of ungulate species present at the various exclosures sites varies widely. All ungulate species present at a site were excluded for the period of study.

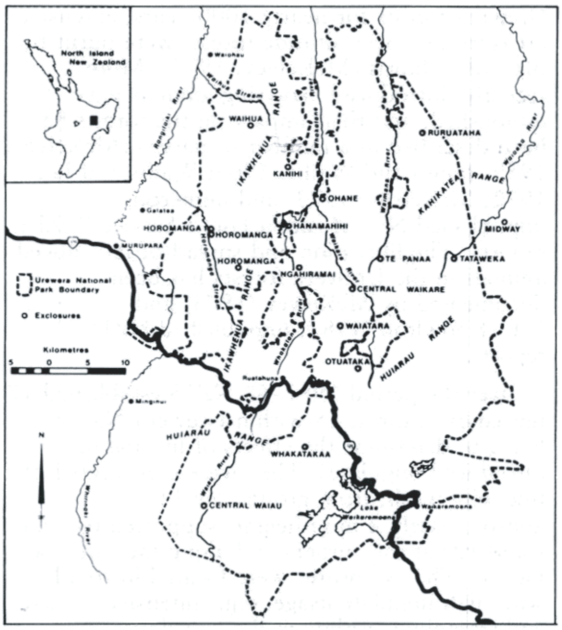

Figure 1: *Map of Urewera forests showing the location of exc/osures.*

Red deer *(Cervus elaphus)* are the most widespread species and were present at all sites when the exclosures were established. Sambar (*C. unicolor),* rusa (*C. timorensis)* and sika (*C. nippon)* deer occur only in parts of the region. It was not possible in this study to differentiate the impact of the various species. In general, deer numbers have declined markedly over the last 10-15 years throughout Urewera forests (Whiting *et al.,* 1980, unpublished NZFS report).

Pigs *(Sus serala)* have long been established in Urewera forests and Wodzicki (1950) assumed that, by 1840, they were established in all suitable habitats. All exclosure sites are within the distribution of pigs. Before 1970 population peaks occurred about every seven years (McKelvey, 1973); recently this pattern has altered and in some areas populations remain in high numbers (Department of Lands and Survey, 1983).

Wild cattle *(Bas taurus)* were last recorded in 1973 (Department of Lands and Survey, 1983) but were largely eliminated before the exclosures were established, although some domestic stock are still grazed in the main valleys. Some sign of cattle has been noted at the Ruruataha and Ngahiramai sites since the exclosures were established.

At present, goats *(Capra hircus)* are found only on the eastern margins of the forest tract (McKelvey, 1973), where they are subjected to intensive control. They are unlikely to have been of any consequence at the exclosure sites.

Approach

Exclosure studies investigate the development of plant communities in the absence of browsing animals. They usually allow the structure and species composition of plant communities which develop in the absence of browsing animals to be compared with those where animals are present. If exclosures are established when animals are already present the vegetation may have been modified from its original state. In this case, the development inside the exclosures will result in a vegetation which mayor may not resemble the original. Fenced exclosures remove browsing animals at a point in time, so that the same combination of factors which exist at this time may not occur again, either on the same site or elsewhere. With these limitations, exclosures do demonstrate the impact of browsing animals on community development over a specific time period.

For the exclosures used in the present study there was little prior information about the vegetation within the exclosures, other than photographs. In this paper the structure (i.e., the numerical distribution of differently-sized individuals for each species) and species composition of the vegetation within the 17 exclosures is compared with that outside, at a particular point in time (summer 1980/81). This information will be interpreted to indicate the effectiveness of recent animal control, and what long term effects continued presence of ungulates may have on Urewera forests.

Methods

During summer 1980/81 a sample plot was located within each of the 17 exclosures, and two adjacent comparable sample plots outside. The tWo control plots were located systematically on areas selected for similar site and forest canopy characteristics as the exclosure plot. The exclosures varied in area from 60 to 100 m^2 and approximated a square or rectangular shape. The plot area within each exclosure (see Appendix 1) was square or rectangular, the length of the sides being the maximum number of multiples of 1.5 m that could be contained within the fenced area. The same plot dimensions were then used for the control plots, so that the design and number of sampling points were constant for all three plots at each site.

Field measurements

Within each plot:

1. In the tree tier (stems with a diameter at breast height over bark (dbhob at 1.4 m) ~ 2.0 cm) the diameter of all stems were measured and recorded by species.
2. In the sapling tier (stems < 2.0 cm dbhob but > 1.4 m tall) the number of stems were recorded for each species. The number of tree ferns with trunks greater than 1.4 m tall were also recorded by species. Lianes were not recorded.
3. The understorey tier (plants < 1.4 m tall) was sampled using 14-25" circular subplots 1 m2 in area, systematically located to cover the plot area. Subplots were established on the ground and, where the sample position fell there, on logs. Within each of these subplots, species were recorded by presence in two height classes; < 15 cm and 15-140 cm.
4. Ground cover was assessed by a systematic coverage of the plot area using point-quadrats (68-100 per plot)*. The top point intercept below 1.4 m was recorded in six classes; non-woody vascular cover, bryophyte, lichen, litter, bare ground and rock. A seventh class, woody cover, was used where the only intercept was the basal portion of a woody plant at ground level.
5. A general description was made. This included a list of species present. Site information recorded included altitude, aspect, slope, percent canopy cover and physiography.

Black and white photographs taken from fixed photopoints were the only previous record of the exclosures. Where possible, temporal aspects of the changes which have occurred are described from retaken photographs.

Analysis

Comparisons between exclosure and control plots were made for various parameters. For each parameter, a mean value for the two control plots at each site was calculated. Statistical comparisons were made using Wilcoxon's signed-ranks test for two groups arranged as paired observations (Sokal and Rohlf, 1969), with each paired observation being the exclosure plot value and the mean value of the control plots for each site.

In comparisons based on individual species, the sites used in the analyses were those where the appropriate species was present in the appropriate height class or tier in at least one of the three plots. In the tree and sapling tiers, density of stems (number per .01 ha) for each species was used to compare exclosure and control plots. In the understorey tier, percent frequency in the two height classes (< 15 cm, 15-140 cm) was used. Species present at less than six sites in the height class or tier being compared were not analysed statistically.

All sites could be used to compare species richness (number of species per .01 ha) between exclosure and control plots because the same area was sampled for the exclosure plot and for each of the control plots at each site. Species richness was compared in the tree tier, both overall and in two classes based on stem diameters; in the sapling tier; and in two height classes (< 15 cm, 15-140 cm) for the understorey tier, with each class being divided into "tree and shrub species" and "other species".

*indicates the range of values used because of different plot sizes.

All sites were used to compare ground cover by percent frequency of the seven cover classes between exclosure and control plots.

Results

Individual tables presented in the results list mean values of the parameters used to compare exclosure and control plots. Significance levels given for the parameter being compared are based on the exclosure plot value and the mean of the control plot values.

Individual species

The mean number of stems per .01 ha for individual species in the tree and sapling tiers in the exclosure and control plots are shown in Table 1. For the more widely distributed species, differences could be tested statistically, but for species present only at a few sites even large differences could not be so tested. Such species will be considered as well as those showing statis.!is:ally significant differences.

A difference in diameter size-class distributions between exclosure and control plots was considered to be the result of an individual species' ability to regenerate after ungulates have been removed. All species listed in Table 1 can be grouped into one of four patterns based on diameter size-class distributions, using only the tree and sapling tier diameter data. These four patterns are illustrated for representative species in Figure 2 (a - d).

The distributions presented for hangehange *(Geniostoma ligustrifolium)* (Fig. 2a) represent the first type of pattern, also shown by *Coprosma australis, C. lucida, C. robusta, C. tenuifolia, Pseudopanax arboreus,* lancewood *(P. crassifolius), P. simplex* and pate (Table 1). These species were absent, or nearly so, in both the tree and sapling tiers outside the exclosures. In the stands sampled, they were characterised as sub-canopy, shade tolerant species, being relatively short-lived with fast growth rates and were often found as epiphytes on canopy trees.

The second type of pattern (Fig. 2b) was shown by mahoe, which was more numerous in the sapling tier inside the exclosures than in the control plots, but showed no difference in the tree tier (Table 1). Rewarewa, putaputaweta, mapau *(Myrsine australis)* and *Pittosporum tenuifolium* showed similar trends (Table 1). Rewarewa was present in the main canopy but the others were sub-canopy species. All are longer lived then those

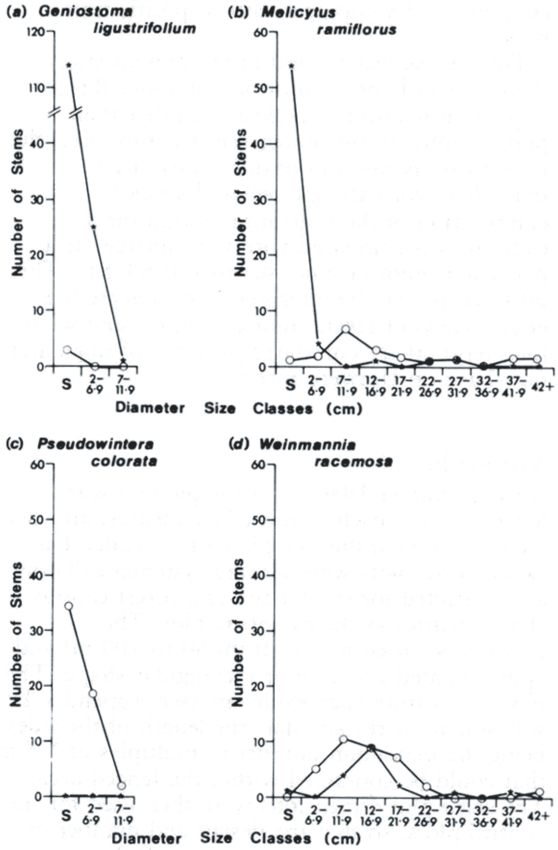

Figure 2: *Number of stems* in *diameter size-classes for exclosure* (*) *and control (o) plots. Representative species are shown, using the data from all sites. The size-classes used are:* S *(saplings) and then* 5 *cm dbhob size-classes for trees.*

included in the first group with hangehange, and only the smaller size-classes showed a difference.

The reverse pattern to that of hangehange was shown by horopito *(Pseudowintera colorata)* (Fig. 2c), which was absent within the exclosures in the tree and sapling tiers but numerous outside at two sites (Table 1). Horopito is a shade tolerant, sub-canopy species in the stands sampled. Photographs taken when the Otuataka exclosure (Appendix 1) was established show seedlings of horopito both inside and outside the exclosure. In this study, horopito was present in the tree and sapling tiers outside the Otuataka exclosure, but still only as seedlings inside the exclosure. At the

Table 1: *Mean number of stems per .01* ha in *the tree and sapling tiers for main canopy and sub-canopy species from the sites where they were found* in *the exc/osure (Exc) and/or control (Con) plots*. For *each species the number of sites (Sites) where present* is *given. Significance levels (p<) are shown for the comparisons between exc/osure and control plots for the more widely distributed species*.

	Trees				Saplings			
Species	Exc.	Con.	Sites	p<	Exc.	Con.	Sites	p<
Main Canopy Species								
Beilschmiedia tawa	1.9	3.8	7	N.S.	1.0	2.2	3	
Dacrydium cupressinum	0.7	1.4	2					
Elaeocarpus dentatus	1.2	0.0	1					
Knightia excelsa	3.5	2.2	4		5.4	0.7	12	.01
Nothofagus fusca	0.9	1.4	2					
N. *menziesii*	2.8	5.9	2		0.0	0.9	1	
N. *solandri* var. *solandri*	4.9	3.7	1					
N. *truncata*					1.3	0.4	2	
Podocarpus dacrydioides					0.0	7.4	1	
P. *totara*	2.5	0.0	1		0.6	0.5	2	
Quintinia acutifolia					3.0	2.2	1	
Weinmannia racemosa	6.2	11.1	5		1.8	0.0	1	
Sub-canopy								
Alectryon excelsus	0.0	0.9	1					
Alseuosmia macrophylla					1.5	0.0	1	
Aristotelia se"ata	7.4	1.8	1		8.8	1.6	2	
Brachyglottis repanda	34.6	11.7	1		42.0	40.7	1	
Carpodetus serratus	3.4	3.0	3		7.4	1.8	9	.05
Coprosma australis	5.3	0.0	10	.01	20.4	0.1	12	.01
C. *ciliata*					1.8	0.0	1	
C. *foetidissima*					3.6	0.0	1	
C. *lucida*	2.4	0.0	3		12.3	0.0	9	.01
C. *rhamnoides*					1.9	0.0	2	
C. *robusta*	7.7	0.8	2		5.0	0.0	2	
C. *rotundifolia*	0.0	0.7	1		29.6	11.8	1	
C. *tenuifolia*	1.5	0.0	2		3.1	0.0	6	.05
Cordyline australis	1.2	.0	1					
Cyathodes fasciculata					87.8	49.0	2	
C. *juniperina*					8.6	4.3	1	
Geniostoma ligustrifolium	13.3	0.0	3		21.5	0.5	8	.01
Griselinia littoralis	0.0	0.9	1					
Gymnelaea cunninghamii					1.2	0.0	1	
Hedycarya arborea	3.0	1.9	2		31.1	0.0	1	
Hoheria sexstylosa	12.3	4.3	1		2.5	2.2	4	
Ixerba brexioides	3.0	3.3	2		1.8	0.0	1	
Leptospermum ericoides	2.8	4.5	2		1.5	1.1	2	
Melicope simplex	0.0	0.7	1		5.8	16.3	2	
Melicytus ramiflorus	1.2	2.2	9.	N.S.	9.5	0.2	9	.01
M *yrsine australis*	0.8	0.6	2		12.1	0.0	4	
M. *divaricata*	0.0	0.6	1		0.0	1.8	1	
Pennantia corymbosa	0.0	1.2	1		3.4	8.9	2	
Pittosporum eugenioides	1.2	0.6	1		6.7	2.2	2	
P. *tenuifolium*	1.8	1.8	1		6.0	0.0	4	
Pseudopanax anomalus (Hook) Philipson					1.4	1.1	2	
P. *arboreus* (Murr.) Philipson	2.5	0.0	1		3.7	0.0	1	
P. *crassifo/ius* (A. Cunn.) C. Koch					9.3	0.0	6	.05
P. *simplex* (Forst. f.) Philipson					3.6	0.0	1	
Pseudowintera colorata	0.0	17.8	2		0.0	29.8	2	
Schefflera digitata	1.8	0.0	5		6.4	0.0	5	
STEMS OF ALL SPECIES	17.5	13.1	17	N.S.	63.2	21.8	17	.01

two sites where horopito was found in the tree and sapling tiers in the control plots, other sub-canopy species were abundant in these tiers within the exclosures. The establishment of fast-growing species such as *Coprosma australis* and pate soon after the exclosures were built has apparently suppressed the growth of horopito inside the exclosures. *Melicope simplex* and *Pennantia corymbosa* (Table 1) appear to show a similar response to horopito to the establishment of the exclosures.

The fourth type of pattern is included to show limitations of the data. Kamahi (Fig. 2d) was found in similar numbers inside and outside the exclosures. In Urewera forests, kamahi has often established in dense "even-aged" stands after fire (Payton, Allen and Knowlton, in press). At least three of the five sites where kama hi was present in the tree and sapling tier represented "even-aged" stands. This is reflected in the diameter size-class distributions presented in Fig. 2d. Because stands of this nature were already present when the exclosures were established and the requirements of kamahi for regeneration are not fulfilled under these dense canopies, no response by this species to the removal of browsing animals would be expected in the exclosures. A similar pattern was shown by *Cyathodes fasciculata* in the sapling tier at two sites (Table 1). At the Horomanga 1 site (Appendix 1), *C. fasciculata* was numerous both inside and outside the exclosure. Photographs taken in 1962 show it was either absent or present only as small seedlings on this site. This species has become abundant both inside and outside the exclosure and its increase may be related to changes in browsing pressure before the exclosure was established.

The densities of three tree fern species. *Cyathea dealbata, C. smithii* and *Dicksonia squarrosa,* were not significantly different between exclosure and control plots (Table 2). *Cyathea medullaris* was present inside the exclosures at three sites, but was absent from the control plots.

The understorey species, for which there was a significant difference in percent frequency between exclosure and control plots in one or both of the understorey tier height classes, are given in Table 3.

Seedlings of the canopy forming species rewarewa and taw a were less frequent in the 15-140 cm height class (Table 3) in the control plots than in the exclosure plots. Tawa is a relatively slow-growing species. With time, it is likely that tawa will show a pattern similar to mahoe (Fig. 2b). Seedlings of the following sub-canopy tree and shrub species were also less frequent in the 15-140 cm height class in the control plots than in the exclosures: *Coprosma australis,* mahoe, mapau, lancewood and pate. The fern *Asplenium bulbiferum* and the liane supplejack *(Ripogonum scandens)* followed this pattern also. However, none of these seven species showed differences between exclosure and control plots in the less than 15 cm height class. This indicates that their seedlings were present outside the exclosures, but height growth is being restricted by browsing.

The short herb *Cardamine debilis,* the woody liane *Metrosideros diffusa,* the orchid *Corybas trilobus* and the adventive herb species *Mycelis muralis* (L.) Dumort were more frequent in the less than 15 cm height class in the control plots than in the exclosures (Table 3). *Uncinia* spp. were more frequent in the 15-140 cm height class outside the exclosures. Photographs taken at intervals since the exclosures were established indicate that these sedge species have increased in cover, both inside and outside the exclosures. This may reflect a response to browsing animals before the establishment of the exclosures.

Table 2: *Mean number of stems (trunks) per .01 ha for tree ferns from the sites where they were found in the exclosure and/or control plots. For each species, the number of sites (Sites) where present is given. Significance levels (p <) for the comparison between exclosure and control plots are shown for the more common species.*

Species	Exclosure plots	Control plots	Sites	p<
Cyathea dealbata	2.6	2.6	9	N.S.
C. *medullaris*	3.7	0.0	3	
C. *smithii*	4.5	3.4	6	N.S.
Dicksonia fibrosa	1.5	0.7	1	
D. *squarrosa*	8.2	3.2	7	N.S.

Species richness

Fewer species were present in the tree tier on the control plots than in the exclosures, when stems in the 2.0 - 6.9 cm diameter size-class and when stems of all diameter sizes were considered (Table 4). These differences were principally because many of the species in the 2.0 - 6.9 cm diameter size-class showed the pattern of response to the absence of browsing animals represented by hangehange (Fig. 2a). To show differences for

Table 3: *Mean percent frequency per plot of understory species in two height classes (less than Hcm and 14-140cm) from sites where they were found in the exclosure (Exc) and/or control (Con) plots in the appropriate height class. Only species showing a significant different in at least one of the classes are listed. Percent frequency was calculated for each plot using the 1m² understorey subplots. For each height class the number of sites (Sites) where a species was present and the significant levels (p<) are given for the exclosure and control plot comparisons.*

	Understorey							
	Less than 15cm				15-140cm			
Species	Exe.	Con.	Sites	p<	Exe.	Con.	Sites	p<
Main Canopy Species								
Beilschmiedia tawa	30.5	20.2	15	N.S.	15.1	6.1	14	.05
Knightia excelsa	20.1	17.0	13	N.S.	20.4	5.8	14	.01
Other species								
Asplenium bulbiferum	6.3	5.0	13	N.S.	8.4	1.9	8	.05
A. flaccidum	5.5	1.9	10	.05				
Cardamine debilis	2.5	15.6	8	.01				
Corybas trilobus	1.7	15.2	6	.05				
Coprosma australis	9.0	3.8	9	N.S.	10.6	1.0	12	.01
Melicytus ramiflorus	12.8	14.4	13	N.S.	15.7	7.3	11	.05
Metrosideros diffusa	28.0	40.5	13	.05	0.0	6.0	2	
Mycelis muralis	1.7	5.3	6	.05				
Myrsine australis	13.5	6.6	8	N.S.	18.1	1.8	11	.01
Pseudopanax crassifolius	3.5	4.9	4		16.7	3.5	6	.05
Ripogonum scandens	13.3	8.7	11	N.S.	15.0	4.6	11	.05
Schefflera digitata	1.0	4.3	4		6.5	0.5	8	.05
Uncinia spp.	35.8	47.6	16	N.S.	11.8	25.7	10	.05

Table 4: *Mean number of vascular species per .01 ha, with associated sample standard deviation in brackets, for exclosure and control plots. Tree tier is given overall and in two classes based on stem diameters. Understorey tier is in two height classes (less than Hcm and H-140cm) for tree and shrub species and all other species, from 1m² circular subplots. Significance levels (p <) are given for the comparison between exclosure and control plots using all sites.*

Tier	Exclosure plots	Control plots	p<
Trees			
d.b.h.o.b. 2.0-6.cm	3.8 (2.87)	1.6 (1.24)	.01
d.b.h.o.b. >7.0cm	2.0 (1.78)	2.7 (1.38)	N.S.
All trees	4.9 (3.41)	3.0 (1.16)	.01
Saplings	12.8 (6.35)	3.2 (2.80)	.01
Understorey			
Less than 15cm			
Tree and shrub seedlings	51.4 (19.7)	54.2 (15.9)	N.S.
All other species	57.9 (28.7)	57.6 (18.5)	N.S.
15-140cm			
Tree and shrub seedlings	45.9 (22.6)	22.8 (17.7)	.01
All other species	22.2 (15.9)	17.9 (13.5)	N.S.

larger (older) trees the exclosures would have to be of greater area and established for a longer time period.

Differences in the sapling tier were more marked (Fig. 3) than those in the tree tier (Table 4) because, in addition to species showing the first pattern of response (Fig. 2a), this tier also included species showing the pattern represented by mahoe (Fig. 2b). Of the 41 species listed in the sapling tier in Table 1, 17 were found only in the exclosure plots whereas four species were found only in the control plots. The low standard deviation for the control plots (Table 4) indicates that species richness in the sapling tier was low at

Figure 3: *Greater species richness and density of stems inside the exc/osure at the Horomanga 2 site.*

most sites outside the exclosures. The Whakatakaa site, located in the floristically poor, relatively high altitude silver beech forest (Appendix 1, McKelvey, 1973), was the only site where there were not fewer species outside than inside the exclosures. The largest differences in species richness in the sapling tier were found at the Kanihi, Horomanga 2 and Horomanga 4 sites (Appendix 1). These were relatively low altitude sites where many of the species less abundant outside the exclosures were present, and included stands dominated by a variety of canopy species (Appendix 1).

The species richness value for tree and shrub seedlings in the 15-140 cm height class in the understorey tier was significantly lower outside than inside the exclosures. This reflects restricted growth by seedlings caused by the effects of browsing animals outside the exclosures. There were no differences for seedlings less than 15 cm.

Ground cover

Although bare ground was only a small part of the total ground cover, its percent frequency was significantly higher outside compared with inside the exclosures (Table 5). Bryophytes were also recorded by more point-quadrats outside than inside the exclosures. The higher value for non-woody vascular plant cover in the exclosure plots (Table 5) would result in fewer intercepts

Table 5: *Mean percent frequency per plot from point quadrats of cover classes for exclosure and control plots. Significance levels (p <) are given for the comparison between exclosure and control plots using all sites.*

Cover class	Exclosure plots	Control plots	p<
Bare ground	0.1	1.1	.01
Litter	40.1	47.0	N.S.
Rock	0.1	0.1	N.S.
Bryophyte	2.6	5.8	.01
Lichen	0.7	0.3	N.S.
Woody cover	17.0	10.1	N.S.
Other vascular plants	39.4	35.6	N.S.

recorded for lower statured cover classes, including bryophytes. However, bryophytes were also recorded on the 1 m2 circular sub-plots at each plot. When the percent frequencies per plot were compared for all sites (as for Table 3), bryophytes were significantly more frequent ($p < .01$) on the control plots.

Discussion

The depletive effects of deer colonizing an area of forest have been described in a number of papers, for example, by Holloway (1950) for forests in western Southland and by Mark and Baylis (1975) for Secretary Island. Usually, the initial impact is the removal of highly palatable sub-canopy species from the tiers which deer can browse. Continued pressure from the browsing animals usually impairs the ability of some species to regenerate (e.g. Johnson, 1972; Veblen and Stewart, 1980) and results in their under-representation, particularly in the lower forest tiers (e.g., Wardle and Hayward, 1970; Wallis and James, 1972). Generally, exclosure studies have shown that such species still have the potential to re-establish when protected from browsing (e.g., Jane and Pracy, 1974; Cuddihy and Stanley, 1978). The results of this study are largely consistent with these findings.

Many of the species more abundant in the forest tiers subject to browse inside the exclosures in this study have also increased inside exclosures built within forests in other parts of New Zealand. These include *Asplenium bulbiferum,* supplejack, *Coprosma* spp., *Pseudopanax arboreus, P. simplex,* lancewood, mahoe, mapau, putaputaweta and rewarewa (Conway, 1949; Jane and Pracy, 1974; Cuddihy and Stanley, 1978). Species more abundant inside the exclosures, in the tiers subject to browse, in this study but not previously reported as increasing inside exclosures include tawa, *Pittosporum tenuifolium* and *Coprosma tenuifolia*.

Many of these more abundant species have been described as being the most palatable ones to deer in the Urewera beech forest shrub storey (McKelvey, 1973), e.g., large-leaved *Coprosma* spp., mahoe, pate and *Pseudopanax* spp.. At Lake Waikareiti in eastern Urewera, there were fewer plants of *Pseudopanax* and *Coprosma* spp. in *Nothofagus* (beech) forest on the mainland than on Rahui Island which was free from introduced animals (James and Wallis, 1969). Wallis and James (1972) considered that deer have inhibited the development of "advance growth" (1.5-3.5 cm diameter class) of red matipo *(Myrsine australis)* and *Melicytus ramiflorus* in northern Urewera, so that these species are understocked in this size class in both the conifer-hardwood and beech forests.

Browsing by deer is inhibiting the regenerative ability of not only the most palatable species present. Knowles and Beveridge (1982) concluded that over most of its range taw a ranked amongst the broad-leaved species of lowest palatability to deer and, McKelvey (1973) considered that it regenerates where browsing prevents beech seedlings from growing. Yet in this study, tawa seedlings, in the 15-140 cm height class (Table 3), were more abundant inside the exclosures suggesting that regeneration of this species was effected by browsing animals outside the exclosures. This is supported by G. Jane (in Knowles and Beveridge, 1982), who considered seedlings and small saplings of tawa had been heavily browsed by deer in parts of the Urewera district. Mapau, putaputaweta and *Pittosporum tenuifolium* are not as highly palatable as, for example, the large-leaved *Coprosma* spp. and *Pseudopanax* spp., yet they show lower abundance in the tiers subject to browse outside the exclosures.

The response inside the exclosures by rewarewa may be only temporary. Greater heights for rewarewa were found inside exclosures by Jane and Pracy (1974), however, rewarewa seedlings declined in density inside exclosures over the period of study (Jane and Pracy, op. cit.). This did not appear to be natural thinning due to competition as in 1980 L. Burrows (pers. comm.) found that rewarewa was absent inside one of these exclosures. It is possible the exclusion of ungulates creates an environment suitable for the early stages of rewarewa growth, but, that subsequently the environment is less suitable.

As the sub-canopy was generally depleted outside the exclosures, opportunities were available for seedlings to establish. An influx of unpalatable species after the depletion of forest understorey has been described in a number of areas (Holloway, 1950; Williams and Chavasse, 1951; McKelvey, 1973). The shrub horopito was more abundant outside than inside the exclosures at two sites in the present study, and McKelvey (1973) described this unpalatable species as increasing in Urewera when deer numbers were high. A few unpalatable species, for example *Cyathodes fasciculata,* have increased as saplings both inside and outside the exclosures. The replacement of normal canopy species by an increase in unpalatable species, especially *Cyathea dealbata* and C. *smithii,* in the understorey has been described by Jane and Pracy (1974). However, these two species were found in similar numbers inside and outside the exclosures in the present study, and most stands outside the exclosures were considered to be understocked with sub-canopy trees and shrubs. Overall, unpalatable woody species did not seem to have replaced palatable species outside the exclosures.

Certain browse-resistant, turf-forming species were significantly more abundant outside the exclosures, and included on adventive species (Table 3). An increase in *Uncinia* spp. has been related to browsing in the Aorangi Range (Wardle, 1967) and in the Tararua Range (Holloway *et al.,* 1963), and for *Cardamine debilis* in the Taramakau catchment (Wardle and Hayward, 1970). Bryophytes were more frequent as ground cover outside the exclosures in the present study. This contrasts with McKelvey's (1973) conclusion that, at the time of his study (when animal numbers were considerably higher), the trampling of hoofs thinned and in some places destroyed the bryophyte-litter cover. At some sites, the greater frequency of herbaceous species outside the exclosures may have reduced the ability of woody seedlings to establish.

Differences between control and exclosure plots found in this study are considered to be primarily the direct or indirect results of browsing by deer. Since the exclosures were established, deer and wild pigs have been the only ungulates of consequence at the sites. The role of wild pigs has not been demonstrated. The results of studies in other areas where deer only are present (Cuddihy and Stanley, 1978; Veblen and Stewart, 1980), are similar to those presented here.

In Orongorongo Valley near Wellington, Fitzgerald (1976) recorded the presence of leaf fragments of hangehange, *Pseudopanax arboreum* (*P. arboreus* (Murr.) Philipson], supplejack and mahoe in the faeces of brushtail possums *(Trichosurus vulpecula)*. Faeces of brushtail possums were present inside the exclosures in the present study but only limited browse was evident. Jane and Pracy (1974) described a similar result, with little utilization of the foliage of palatable species by brushtail possums inside exclosures.

The results of this study were influenced by the structure and species composition of the stands at the sites sampled and the regenerative behaviour of individual species on these sites. These stands had relatively closed canopies, and most of the differences between exclosure and control plots were contributed by relatively shade-tolerant species which are normally sub-canopy species in such forest. The canopy-forming species tawa was an exception. However it is shade tolerant and may "regenerate continuously" (Knowles and Beveridge, 1982). The lack of a difference between exclosure and control plots for a species did not necessarily indicate that the presence of ungulates is not inhibiting the ability of a species to regenerate. Because of the small exclosures used the results of the present study are limited, particularly in accounting for the regeneration of large canopy species. Natural stand dynamics also had an important effect on the results obtained.

Exogenous factors other than introduced mammals have been important in determining the structure and composition of Urewera forests. Canopy disturbance is sometimes important in the initiation of the regenerative phase for a species; this is often so for canopy species (e.g., Wardle, 1974). For example, in this study, the sites at which kamahi was present were mainly dense-canopied, "even-aged" stands probably established after fires. A difference between exclosure and control plots was not found for kamahi as it does not regenerate in such stands. Since deer have become established, the formation of these "even-aged" kamahi stands on burn sites has been inhibited. Kamahi is palatable to deer; McKelvey (1955) in a description of succession after fire at Te Whaiti and Payton *et al*. (in press) in a study of post-fire succession in the Waikare catchment considered ungulate browsing had prevented the establishment of kamahi. If the exclosures had been located on disturbed sites, e.g., where there were large canopy gaps, it is possible that differences between exclosure and control plots would have been evident for more of the main canopy species.

A large number of fenced exclosures have been established in indigenous forests throughout New Zealand to demonstrate response to the removal of browsing ungulates. In general, exclosure plots have been located on stable sites with intact canopies. Because of this, most studies have usually shown responses by palatable, relatively shade-tolerant sub-canopy species. It is important, therefore, that the regeneration ecology of individual species is accounted for in the design of exclosure studies (Veblen and Stewart, 1982).

From the structural analysis of canopy and sub-canopy species, it can be predicted that long-term modification of forest structure and composition in the study area will take place if the present level of animal use continues. Highly palatable, often short lived sub-canopy species (.e.g, *Coposma australis)* had been virtually removed from the understorey before the exclosures were established. This study has shown that over the last 13-20 years, these species, along with less palatable ones, have developed again in the lower forest tiers inside the exclosures. For some longer-lived species (e.g., mapau), the effect of browsing animals is indicated by the under-representation of larger seedlings, saplings and small trees outside the exclosures. This under-representation is found only in a small part of the diameter range of an individual species, and is related to the length of time ungulates have been present (Fig. 2b). The subsequent modification to the forests will depend upon the degree to which a species is under-represented. If the presence of animals continues at a level similar to that at present, a species such as mahoe, virtually absent outside the exclosures as saplings, will decline in abundance through all size classes. Although mahoe occurred in the sub-canopy in the stands sampled, it is a dominant canopy species on unstable sites, including steep mid-slope areas and alluvial fans.

Small seedlings, of species less abundant in the sapling tier and as small trees (dbhob 2-6.9 cm) in the control plots, were present outside the exclosures. Seed sources of longer-lived species were still present within the stands. But for species absent in stands as mature plants, seed must come from plants established as epiphytes and on bluffs beyond the reach of browsing animals. Sub-canopy tree and shrub species less abundant outside the exclosures were often noted as epiphytic seedlings on tree fern trunks *(Cyathea* spp. and *Dicksonia* spp.) and in the crowns of larger trees outside the exclosures. These included *Pseudopanax arboreus,* pa.te and *Coprosma lucida*. On some sites turf-forming species in particular, were more abundant outside the exclosures and may limit the establishment of sub-canopy species. However, the presence of seedlings outside the exclosures (Table 3) indicates that a response similar to that inside the exclosures would take place, at most sites, with the removal of ungulates.

In general, deer and other ungulate densities have been reduced markedly throughout most of the Urewera forests over the period of the present study (Whiting *et al.,* 1980, unpublished NZFS report). Even with this reduction, the ability of certain species to regenerate is being inhibited. Our observations suggest the results of this study are widely applicable to similar stands throughout the Urewera forests.

Acknowledgements

For assistance in the field we thank Rotorua Conservancy staff and the field party leader, J. Manhire; for assistance in the field and data analysis, M. Kennett and R. Morison; and, assistance in data analysis, P. Cromarty. We thank K. Platt for help with plant identification, M. McBride for drawing the figures, J. Orwin for editing, and J. Wardle, A. Rose and C. J. Burrows for reviewing the manuscript.

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Appendix 1: *List of exclosures.*

Size	Grid Reference*	Year established	Dominant canopy species over the exclosure‡	Altitude	Aspect	Slope	Plot size used (m)
Waihua	N 86 345830	1968	*Dacrydium cupressinum* *Podocarpus spicatus* *Beilschmiedia tawa*	400	60°	0°	9.0 x 7.5
Ruruataha	N 87 589817	1968	*Pittosporum eugenioides* *Melicytus ramiflorus*	300	63°	6°	9.0 x 9.0
Kanihi	N 87 399768	1968	*Leptospermum ericoides* *Knightia excelsa*	380	300°	15°	7.5 x 7.5
Ohane	N 87 447725	1967	*Weinmannia racemosa* *Melicytus ramiflorus*	300	190°	29°	9.0 x 7.5
Midway	N 87 708686	1963	*Weinmannia racemosa* *Melicytus ramiflorus*	760	330°	23°	9.0 x 7.5
Hanamahihi	N 87 397678	1967	*Beilschmiedia tawa* *Melicytus ramiflorus*	300	255°	30°	7.5 x 7.5
Horomanga (1)	N 86 284677	1961	*Nothofagus solandri* *Knightia excelsa*	300	295°	16°	9.0 x 9.0
Horomanga (2)	N 86 285673	1961	*Beilschmiedia tawa* *Melicytus ramiflorus*	300	250°	26°	9.0 x 7.5
Te Panaa	N 87 528640	1966	*Weinmannia racemosa* *Knightia excelsa*	380	275°	17°	7.5 x 7.5
Tataweka	N 87 634638	1963	*Podocarpus spicatus* *Beilschmiedia tawa*	530	310°	4°	9.0 x 9.0
Horomanga (4)	N 86 122621	1961	*Nothogagus fusca* *Weinmannia racemosa*	490	195°	5°	12.0 x 4.5
Ngahiramai	N 87 406618	1963	*Dacrydium cupressinum* *Beilschmiedia tawa*	260	215°	9°	9.0 x 9.0
Central Waikare	N 96 488588	1966	*Beilschmiedia tawa* *Melicytus ramiflorus*	300	95°	4°	7.5 x 7.5
Waiatara	N 96 473534	1967	*Dacrydium cuppressinum* *Beilschmiedia tawa*	490	90°	26°	9.0 x 7.5
Otuataka	N 96 497474	1968	*Nothofagus menziesii* *Nothofagus fusca*	830	350°	5°	7.5 x 7.5
Whakatakaa	N 96 423354	1963	*Nothofagus menziesii*	1130	195°	6°	9.0 x 9.0
Central Waiau	N104 276275	1968	*Beilschmiedia tawa*	550	135 °	5°	9.0 x 9.0

* Using New Zealand Mapping Series 1 (inch to the mile) topographical map.
‡ Recorded ongeneral plot description.