

Forestry Research Centre, FRI, P.O. Box 31-011, Chri~tchurch, New Zealand.

¹ Present address: P.O. Box 40, Oxford, Canterbury.

FOREST UNDERSTOREY CHANGES AFTER REDUCTION IN DEER NUMBERS, NORTHERN FIORDLAND, NEW ZEALAND

Summary: High deer numbers in northern Fiordland in the 1960s significantly changed forest understorey composition. The density of woody plants in the understorey was reduced in some areas by as much as 50%, and preferred plants became less abundant than those seldom eaten. However, the impact of deer and wapiti varied between forest types. Seral communities and silver beech forests at low altitudes in the unmodified Milford/Bligh Sound area had high proportions of preferred plants in the understorey, and these were the types that were more modified by browsing pressure than those growing at high altitudes or on poor soils.

A resurvey of the Wapiti, Doon, and Glaisnock catchments in 1984/85 showed that densities of woody plants in the forest understorey had increased on average by at least 75% after a c. 80% reduction in deer numbers since earlier surveys (1969 and 1975). Woody food plants highly preferred by deer were rare in most forest types in 1969, but were present in all types by 1984 and had increased in density by as much as 300-400%. However, recovery was still largely confined to understorey tiers < 75 cm high and most of the recovery had occurred since 1975. Proportions of highly preferred species in the understorey of these forests had not reached those recorded in unmodified forests in the Milford/Bligh Sound area in 1969.

Keywords: browsing damage; beech/hardwood forests; permanent quadrats; preferred plants; red deer; wapiti; understorey composition; unmodified forests; variable area plots; Fiordland.

Introduction

Because few forests in New Zealand have escaped modification by introduced animals, it is often difficult to separate their effects from natural changes (Veblen and Stewart, 1982). One approach is to compare forest composition in geographically similar areas with different animal histories. Since the introduction of deer into Fiordland early this century, catchments in northern Fiordland have been colonised at different times (Wardle, 1984). They thus provide suitable areas for a comparative study of the impact of deer on understorey development (e.g., Wardle, Hayward and Herbert, 1971; Wardle, 1984). In 1969/70 the Milford/Bligh Sound area was in the initial stages of deer colonization and was largely unmodified. The density of woody plants in the browse tiers of the understorey provided a benchmark for interpreting animal effects in similar areas with different deer histories. The forest understoreys in the Wapiti, Doon, and Glaisnock catchments (eastern 'Wapiti Area') were being heavily browsed by deer in 1969/70 and were severely depleted (Wardle *et al.*, 1971).

Since the early 1970s, deer numbers have been reduced by airborne hunting, and in 1984 numbers were comparatively low (Nugent, Parkes, and Tustin, 1987). Resurveys in the Wapiti, Doon, and Glaisnock catchments in 1975/76 and 1984/85 gave an opportunity to monitor changes in forest structure and composition after a marked decline in deer numbers.

The 1969/70 Milford/Bligh Sound data provided a baseline for assessing the degree of modification of the Wapiti/Doon/Glaisnock forests. This paper therefore aims to:

1. Determine changes in structure and composition of the Wapiti/Doon/Glaisnock forests since the 1969 and 1975 surveys;
2. Ascertain how much of the change can be attributed to reductions in deer populations;
3. Determine the extent to which the forests differed from an unmodified state; and
4. Identify forest types where deer were still influencing composition, structure, and regeneration.

Methods

Changes in understorey composition and structure in Wapiti, Doon, and Glaisnock forests 1969-1984

In 1969, the understorey tiers were measured on 117 variable area plots along 20 randomly located altitudinal transects within the Wapiti, Doon, and Glaisnock catchments (Table 1). From a randomly located plot centre a line was run out to a specified radius (0.55, 0.90, 1.25, 1.80, 2.50, or 3.10 m) until at least 10 woody individuals in the browse tier (0.3-1.8 m) were counted. Sociological and site descriptions at each plot allowed pooling of data for various forest types, landforms, altitudes, aspects, and slopes. In 1984, 531 similar variable area plots were sampled in a

Table 1: *Distribution of variable area plots used in study. Forest type after Wardle et al. (1971).*

AREA	*FOREST TYPE.									TOTAL
	C1	C2	C3	C4	M1	M2	M3	P2	P3	
<i>Plots Measured in 1969</i>										
Glaisnock	16	14	3	1	-	-	-	20	-	54
Wapiti/Doon	16	14	3		10	6	5	9	-	63
Milford/Bligh	9	18	1	49	31	7	10	3	20	148
<i>Plots Measured in 1984</i>										
Glaisnock	24	58	78	-	5			13	-	178
Wapiti/Doon	45	38	66	-	53	39	40	56	-	353

- *C1 Silver beech-*Archeria-Senecio* forest
 C2 Silver beech-*Coprosma* forest
 C3 Silver beech-pepperwood-*Blechnum* forest
 C4 Kamahi-silver beech-*Cyathea* forest
 M1 Silver beech-rata-kamahi-mountain beech forest
 M2 Mountain beech-*Phyllocladus* forest
 M3 Mountain beech-manuka-*Dacrydium* forest
 P2 Silver beech-lacebark-*Polystichum* forest
 P3 Mahoe-pate-*Cyathea* forest

separate study on deer habitat and the physical environment (Stewart and Harrison, 1987). Sufficient information on stand composition and the physical environment was gathered to categorize the data into forest types and landform classes (Table 1). The results from 1969 and 1984 were compared to assess changes in understorey density and composition.

Changes in the understorey from 1975 to 1984 were also measured on seedling plots in 24 permanent 20 x 20 m quadrats (Allen and McLennan, 1983), established in 1975 and remeasured in 1984 in the Wapiti and Doon catchments. These quadrats were evenly spaced along altitudinal transects and located in forest types identified from the 1969 survey (Wardle *et al.*, 1971). This allowed an alternative and independent assessment to the variable area plot survey.

Woody species in the understorey were divided into three groups based on food preferences of deer (Table 2). The least preferred group includes species seldom eaten even where no alternative food is available. These groupings were based on browse pattern data from the 1969 survey (Wardle *et al.*, 1971; Wardle, 1984) supplemented by information on how food patterns change as deer populations irrupt (Holloway, 1950; Mason, 1951; Mark and Baylis, 1975; Wardle, 1984). These groupings were used to assess deer-related changes in the forest understoreys.

Changes in deer diet 1969-1984

Plant species browsed by deer and intensity of browsing were recorded on 51, 59, and 58 reconnaissance plots (Allen and McLennan, 1983) in the Wapiti Doon catchments in 1969, 1975, and 1984, respectively. Plots were located along the same altitudinal transects for each survey. Browse indices (Wardle *et al.*, 1971) were calculated to assess whether the feeding pattern of deer changed as population levels declined.

Forest under storey composition in the unmodified Milford/Bligh Sound forests

In 1969 the understorey tiers most affected by deer were sampled by counting the number of stems 0.3 to 1.8 m tall for all woody species on 148 variable area plots (Table 1). The results formed a comparative base for assessing the degree of recovery of forest types in the Wapiti, Doon, and Glaisnock catchments after the reduction of deer populations.

Results

Changes in under storey composition and structure in Wapiti, Doon, and Glaisnock forests 1969-1984.

- a) Changes in understorey on variable area plots 1969-1984

In 1969 deer had had most impact on understoreys in

Table 2: Groupings of woody plant species within three food preference categories for deer.

Highly Preferred	Moderately Preferred	Least Preferred
<i>Aristolelia serrata</i>	<i>Aristolelia fruticosa</i>	<i>A rcheria traversii</i>
<i>Carmichaelia grandifolia</i>	<i>Coprosma astonii</i>	<i>Clematis paniculata</i>
<i>Carpodetus serratus</i>	<i>C. ciliata</i>	<i>Cyathodes juniperina</i>
<i>Coprosma lucida</i>	<i>C. colensoi</i>	<i>Dacrydium biforme</i>
<i>Fuchsia excorticata</i>	<i>C. foetidissima</i>	<i>D. intermedium</i>
<i>Griselinia littoralis</i>	<i>C. pseudocuneata</i>	<i>Dracophyllum longifolium</i>
<i>Hedycarya arborea</i>	<i>C. rhamnoides</i>	<i>D. menziesii</i>
<i>Hoheria glabrata</i>	<i>C. rotundifolia</i>	<i>D. uniflorum</i>
<i>Meliccytus ramiflorus</i>	<i>C. rugosa</i>	<i>Elaeocarpus hookerianus</i>
<i>Myrsine australis</i>	<i>Hebe odora</i>	<i>Freycinetia banksii</i>
<i>Pseudopanax colensoi</i>	<i>H. salicifolia</i>	<i>Gaultheria antipoda</i>
<i>Pseudopanax crassifolius</i>	<i>Myrsine divaricata</i>	<i>G. rupestris</i>
<i>Ripogonum scandens</i>	<i>Nothofagus solandri var. eliffortioides</i>	<i>Leptospermum scoparium</i>
<i>Schefflera digitata</i>	<i>N. menziesii</i>	<i>Metrosideros diffusa</i>
<i>Senecio bennettii</i>	<i>Olearia arborescens</i>	<i>M. umbellata</i>
	<i>O. ilicifolia</i>	<i>Neomyrtus pedunculata</i>
	<i>Pennantia corymbosa</i>	<i>Olearia colensoi</i>
	<i>Pit/osporum colensoi</i>	<i>Phylloeladus alpinus</i>
	<i>Pseudopanax anomalus</i>	<i>Pit/osporum crassicaule</i>
	<i>P. linearis</i>	<i>Podocarpus hallii</i>
	<i>P. simplex</i>	<i>P. ferrugineus</i>
	<i>Rubus cissoides</i>	<i>Pseudowintera colorata</i>
	<i>Weinmannia racemosa</i>	

forest types growing on seral sites (e.g., silver beech-lacebark-*Polystichum*² forest, P2) and at low altitude (e.g., silver beech-pepperwood-*Blechnum* forest, C3) and least in those on poor soils (e.g., mountain beech types, M2, M3; Wardle *et al.*, 1971).

Mean stem density in the Wapiti/Doon/Glaisnock seral and silver beech forests (high altitude silver beech forests, C1, C2) did not change significantly from 1969 to 1984 (Table 3). However, stem density increased significantly in mountain beech types (M1, M2, M3) and included the appearance of, or marked increases in, highly preferred species (e.g., *Pseudopanax crassifolius*, *P. colensoi*; Table 3). Highly preferred species, notably *Pseudopanax crassifolius*, *P. colensoi*, and *Griselinia littoralis*, also appeared in type C3 (silver beech-pepperwood-*Blechnum* forest). The high altitude communities (C1 and C2) and the seral community (P2) showed the least change.

(b) Changes in understorey on permanent quadrats 1975-1984

The number of species in the understorey had increased substantially since 1975, e.g., 29 woody

species were recorded in the <15 cm tier in 1975 and 38 in 1984; 28 species were recorded in the 16-135 cm tiers in 1975 and 40 in 1984. This was accompanied by an almost universal increase in the densities and frequencies of individual species. Thirty-seven of the 40 species in the 16-135 cm tiers, increased markedly in density, e.g., *Pseudopanax simplex* from 496 to 3245 stems/ha (550% increase), *Hoheria glabrata* from 68 to 437 (540%), *Griselinia littoralis* from 90 to 345 (280%), and *Coprosmafoetidissima* from 2164 to 3982 (85%). *Aristolelia serrata*, *Fuchsia excorticata*, *Schefflera digitata* and a number of other species not recorded in the 16-135 cm tiers in 1975 were present in 1984. Some of the least preferred species also increased, but proportional increases were not as much as for preferred species, e.g., *Pseudowintera colorata* increased from 2728 to 3521 stems/ha (29%).

The above increases in density were largely confined to the 16-75 cm tiers. Increases in tiers above 75 cm were small by comparison, indicating that recovery after the reduction of deer numbers was not complete.

Large increases in frequency also occurred for almost all species. Thirty-six of the 38 woody plant

² Nomenclature follows Allan (1961), Moore and Edgar (1970), and Edgar (1973).

Table 3: Mean density (per ha, \pm S.E.) of all woody stems, and highly preferred stems in the understorey (30-180 cm) of forest types in the Wapiti, Doon, and Glaisnock catchments in 1969 and 1984.

	FOREST TYPES				
	Seral P2/3	Silver Beech		Mountain beech	
		C3/4	C1/2	M1	M2/3
n (1969)	29	7	60	10	11
n (1984)	69	144	165	58	79
ALL STEMS					
1969	13477 \pm 2330	22381 \pm 7754	19825 \pm 2675	11633 \pm 3402	30818 \pm 9714
1984	10130 \pm 1460	30767 \pm 3464	23104 \pm 1540	22334 \pm 3934	50010 \pm 5137
HIGHLY PREFERRED STEMS					
1969	1414 \pm 1239	-	1621 \pm 695	-	-
1984	1691 \pm 624	2780 \pm 657	1389 \pm 298	1055 \pm 357	1730 \pm 730

species in the < 15 cm tier showed frequency increases of c. 80-400%, e.g., in the <15 cm tier *Griselinia littoralis* increased from 7 to 31%, *Hoheria glabrata*, 9 to 20%, *Pseudopanax simplex*, 14 to 26%, and *Coprosma foetidissima* 16 to 30%. In comparison, the least preferred species *Pseudowintera colorata* increased slightly from 10 to 13%.

Some herbs and ferns (e.g., *Polystichum vestitum*) that were present only in the < 15 cm tier in 1969 had not changed in their frequency of occurrence but had increased in height to be present in the 16-135 cm tiers in 1984.

Changes in deer diet 1969-1984

As preferred plants became more available in the understorey they formed an increasing proportion of deer diet (Table 4). Changes in the mean browse index indicated that browsing declined as deer numbers were reduced.

Griselinia littoralis was the major woody food plant in the Wapiti/Doon in both 1969 and 1984 (10070 of total browse in 1969, 32% in 1984), and *Pseudopanax simplex* was also a major component of the diet (7% of total browse in 1969 and 1984). However, proportions of other species in the diet changed from 1969 to 1984. *Coprosma foetidissima*, *Pseudopanax linearis*, and *Myrsine divaricata* each provided 7 or 8% in 1969 but individually accounted for < 1% in 1984. *Coprosma ciliata* and *Hoheria glabrata* (3% of total browse and unbrowsed in 1969, respectively) each provided 6% of total browse in 1984.

The proportion of woody species in the diet decreased from 84% in 1969 to 68% in 1984, e.g., small-leaved *Coprosma* spp. provided c. 27% of the

Table 4: Changes in feeding patterns of deer between 1969, 1975, and 1984 in the Wapiti/Doon. The apparent composition of the diet, as determined from browse indices, is given as percentages. MBI (Mean Browse Index per plot) calculated after Rose and Burrows (1985).

Browse preference category	Year		
	1969 (n=51)	1975 (n = 59)	1984 (n = 58)
WOODY SPECIES			
highly preferred	22	16	42
moderately preferred	56	60	23
least preferred	6	2	3
TOTAL	84	78	68
HERBACEOUS SPECIES	16	22	32
MBI	7.4	3.7	1.2

diet in 1969 but only 14% in 1984. This decrease in the proportion of woody plants was compensated for by an increase in the proportion of the fern *Polystichum vestitum* (2% of total browse in 1969, 29% in 1984). However, some ferns and herbs browsed by deer in 1969 (notably *Todea superba*, 5% and *Astelia nervosa*, 6%) were less browsed in 1984 (3% and 0%, respectively).

Current status of the forests

(a) Unmodified baseline - Milford/Bligh Sound

The density of all understorey woody stems was lowest in the seral types, higher in silver beech types, and highest in mountain beech types (Table 5). Highly preferred species (Table 2) comprised the largest proportion of stems in the seral types, progressively

Table 5: Density of woody stems (per ha) in the understorey (30-180 cm) in unmodified forests of the Milford/Bligh Sounds (1969). n = number of variable area plots. * numbers followed by a different letter are significantly different at $P < 0.05$ according to a t-test.

	FOREST TYPES					
	Serai	Silver beech			Mountain beech	
		P2/3	C3/4	C1/2	M1	M2/3
n	2	3	50	27	1	17 3
Density (all stems)		12029a*	19410bc	27191c	56032de	45824e
Density (highly preferred species)		7964a	6443b	4247b	7441ab	471c
% highly preferred species		66	33	16	13	1

declined through silver beech types, and comprised only 1% of stems in M2/M3 (Table 5). Generally, the seral types also had the highest density of most preferred plants, silver beech types at low altitude lower densities and mountain beech types the lowest (Table 5). This gradient in the proportion of preferred species across forest types has been related to a decline in soil nutrient status (Stewart and Harrison, 1987).

An exception was type M1 that supported similar densities of highly preferred plants to the seral types. Although highly preferred species occurred at similar densities in P2/P3 and M1 they made up a much lower proportion of the total stems in M1 (Table 5). Therefore browsing by ungulates could adversely affect P2/P3 but might not be as critical in M1 where many species of lower preference could replace highly preferred species.

(b) Density of the understorey

In both the Wapiti/Doon and Glaisnock the mean overall stem densities of the understorey in most forest types were not significantly lower than the Milford/Bligh Sound area (Fig. 1a). This suggests that in most types the understorey density had recovered to pre-deer levels. The large differences between the Milford/Bligh and Wapiti/Doon M1 forests may reflect continued deer use. M types were rare in the Glaisnock (Table 1) and separate comparisons for this area could not be made.

C3 forest in the Glaisnock had a significantly higher understorey stem density than either of the other areas. This may be related to higher densities associated with higher soil nutrient status on frequently disturbed sites in the Glaisnock compared to C3 forests on more stable sites in the Wapiti/Doon (Stewart and Harrison, 1987).

(c) Understorey composition

The proportions of highly preferred plants increased significantly in the Wapiti/Doon/Glaisnock from 1969 to 1984. However, the Milford/Bligh Sound results

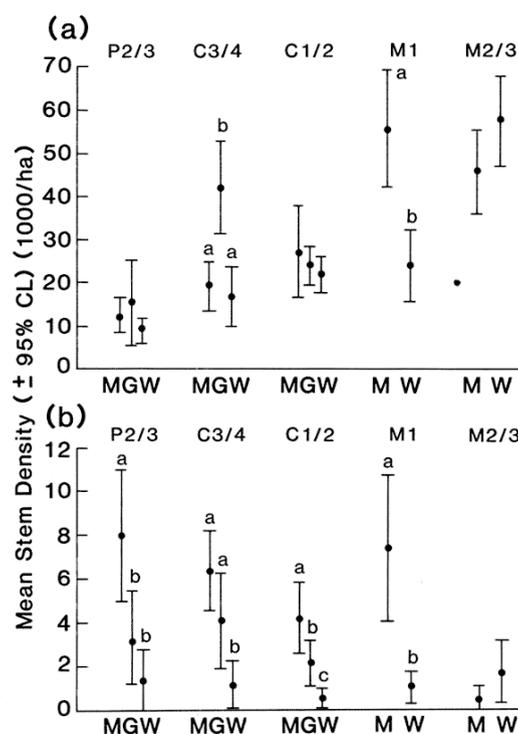


Figure 1: Mean density of (a) all woody stems, and (b) highly preferred stems, in the understorey (30-180 cm) of forest types in the Milford/Bligh Sound (M) in 1969, and the Olaisnock (O), and Wapiti/Doon (W) catchments in 1984. Bars followed by different letters are significantly different between area comparisons at $p < 0.05$ (t-test).

show that the shift to highly preferred plants was incomplete (Fig. 1b). The density of highly preferred plants in M1 understoreys was still significantly lower in the Wapiti/Doon than in unmodified forests (Fig.

1b). In P2/3, C3/4, and C1/2 forests, stem densities of highly preferred plants in the Glaisnock were closer to those in unmodified Milford/Bligh than were those of the Wapiti/Doon.

Proportions of most preferred plants were higher in all forest types (except M2/M3) in Milford/Bligh Sound than in the Wapiti/Doon/Glaisnock in 1969 or 1984 (Table 6). The proportions of highly preferred species decreased from P2/3, C3/4, C1/2, M1, to M2/3 in all three areas, reflecting an increase in soil development and a decrease in drainage (Stewart and Harrison, 1987).

Table 6: Percentage of highly preferred species in the understorey (30-180 cm) of forests in Milford/Bligh Sounds, and the Wapiti/ Doon/Glaisnock.

	FOREST TYPES				
	Seral P2/3	Silver beech C3/4	Mountain beech C1/2 MI		M2/3
Milford/Bligh Wapiti/Doon/ Glaisnock (1984)	66	33	16	13	
Wapiti/Doon/ Glaisnock (1969)	17	9	6	5	3
Wapiti/Doon/ Glaisnock (1969)	11	0	8	0	0

The largest difference in the proportion of highly preferred plants between Milford/Bligh Sound and the Wapiti/Doon/Glaisnock was in P2/3, indicating that this type was the most modified. The current low proportions of highly preferred plants in C3 and M1 also indicates strong modification. The effects of deer on forest under storey composition therefore remain most pronounced in seral forests, low and mid altitude silver beech forests, and in silver beech-rata-kamahimountain beech. Their effects are least pronounced in high altitude silver beech forest (C1/2) and in forests on poorly drained and infertile soils (M2 and M3).

Proportion of forest types/catchment

As variable area plots were installed at fixed intervals along randomly located altitudinal transects in the 1969 survey, the proportion of plots in each forest type should approximate the proportion of forest types in each area. Almost 40% of variable area plots in the Glaisnock occurred in seral forest types compared with 16% for Milford/Bligh Sound and 8% for the Wapiti/Doon (Table 7). Conversely, the Wapiti/Doon had the highest, and the Glaisnock the lowest, proportion of plots in mountain beech types growing on poor soils (Table 7). Understorey stem densities attainable in the absence of deer would

therefore be expected to be much lower in the Glaisnock than in the Wapiti/Doon. However, in the Glaisnock, higher proportions of these stems would be highly preferred species and these forests would be more likely to be influenced by deer than those of the Wapiti/Doon.

Table 7: Proportion of 1969 variable area plots in the major forest types of Milford/Bligh Sounds, Wapiti/Doon, and the Glaisnock.

FOREST TYPE	% Frequency			Total
	Milford/ Bligh S.	Olaisnock	Wapiti/ Doon	
Seral (P) types	16	40	8	25
Silver beech (C) types	52	56	55	56
Mountain beech (M) types	32	4	37	19

Discussion

The marked increases in woody understorey density and number of preferred species since 1969 largely reflected an 80% reduction in deer numbers (Nugent *et al.*, 1987). In 1969 when deer numbers were high, the forests were severely depleted and highly preferred species were rare in many forest types (Fig. 2). Deer numbers had declined significantly by 1975, especially in the Glaisnock catchment (c. 75%), as a result of airborne hunting (Nugent *et al.*, 1987). Feeding patterns of deer indicated that understoreys had not recovered significantly by 1975 (Table 4). By 1984, however, overall stem densities were high, and highly preferred species in the browse tier numbered > 1000/ha in all forest types (Fig. 2). Deer numbers and browsing intensity (mean browse index = 1.2) were very low by 1984.

The most modified forest types in 1984 (P2, M1, C3) contained the most deer (Nugent *et al.*, 1987). These forests were also some of those being heavily utilised in 1969 (Wardle *et al.*, 1971). High altitude silver beech forests (C1/C2), moderately utilized in 1969 (Wardle *et al.*, 1971; Wardle, 1984), were little modified and contained few deer in 1984 (Nugent *et al.*, 1987). Lowest deer densities in 1984 were found in M2/M3 forests (Nugent *et al.*, 1987), types characterized by few highly preferred species on infertile sites (Stewart and Harrison, 1987).

Comparison of the Wapiti/Doon/Glaisnock understoreys with those of the largely unmodified

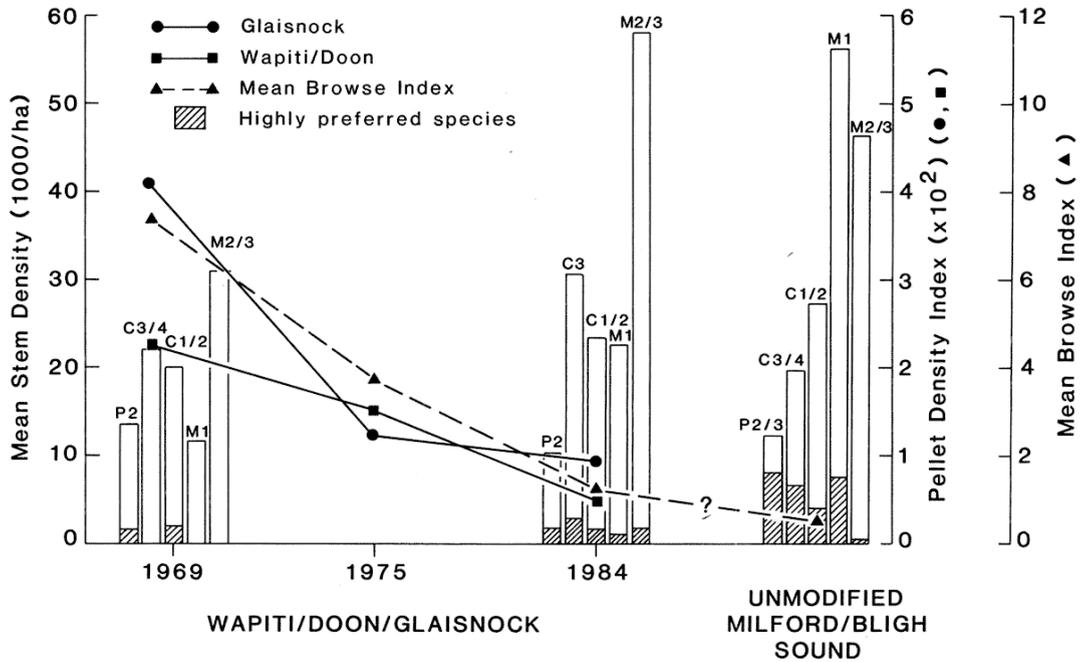


Figure 2: Mean density of all woody stems and highly preferred stems in the understorey of forest types of the Wapiti/Doon/Glaisnock and Milford/Bligh Sound catchments in 1969 and 1984 in relation to changes in deer numbers (from Nugent *et al.*, 1987) and the mean browse index (Rose and Burrows, 1985).

Milford/Bligh Sound area indicated trends in recovery (Fig. 2). It is unlikely, however, that understoreys in the Wapiti/Doon/Glaisnock will ever attain a similar composition to those in the Milford/Bligh Sound. Although the comparison between the two areas indicated valid trends for groups of variously preferred species, individual differences in species composition between some types are likely to exist, e.g., C3/4 in Milford/Bligh Sound contains some coastal species not present in C3 forest of the Wapiti/Doon/Glaisnock (1984). Similarly, slight differences in overall stem density would be expected between types in different areas (Fig. 2).

In 1984, deer pellet group densities by forest type in order of declining density were P1/2, C3, M1/2, C1/2 and M3 (Nugent *et al.*, 1987). The utilization of these forest types by deer is related to the underlying physiography and soil nutrient status (Stewart and Harrison, 1987). In 1984 terraces and toe slopes were the most used, followed by ridges/spurs/benches, sideslopes and, finally, block fields and moraines

(Nugent *et al.*, 1987). Landforms that are readily accessible to deer and contain many preferred species (e.g., P2 forest on debris cones or C3 forest on terraces) are still being utilised. As well as influencing forest understoreys on recent soils (P2, C3), deer occasionally browsed in areas that they lie up in or use as travel corridors, such as mid altitude silver beech forests (C2) and along ridges and benches in M1 forest.

Deer numbers in the Glaisnock in 1969 were much higher than in the Wapiti/Doon (Fig. 2; Nugent *et al.*, 1987). The recovery of highly preferred stems in the understorey by 1984 however, was much greater in the Glaisnock (Fig. 1b). This is probably due to differences in the proportions of seral (P2) and low-mid-slope silver beech forests (C3/2) on different landforms in the two areas (Stewart and Harrison, 1987). For instance, a high proportion of P2 and C3 forests in the Wapiti/Doon were on terraces at low altitude that were still being utilised by deer in 1984. Conversely, in the Glaisnock more than 50% of C3

plots were on colluvial sideslopes where deer had been significantly reduced (Stewart and Harrison, 1987; Nugent *et al.*, 1987).

Although deer have important influences on forest understoreys, changes in the overstorey also influence understorey development. However, little change occurred in overstorey composition or structure in the 24 permanent quadrats between 1975 and 1984 (mean basal area 68.1 m² and 68.2 m², mean stem density 2970 and 2680/ha, respectively) (Wardle and Stewart, 1986). Individual quadrats showed changes in basal area ranging from losses of 13% to gains of 12%, and changes in overstorey stem density from increases of 8% to decreases of 36%. Highly preferred plants increased in the understorey of all quadrats but showed the greatest increases in quadrats with decreasing basal area (Wardle and Stewart, 1986). The responses to small changes in basal area suggest that some of the understorey recovery could be attributed to changes in the overstorey rather than the changing pattern of deer use. However, the magnitude of the changes in stem density from 1969 to 1984 suggests that the reduction in browsing pressure was the major factor responsible for understorey recovery.

Differences in understorey composition make certain forest types more vulnerable to animal browsing than others. Seral types are the most susceptible since most of the species in the understorey and many of the canopy species that regenerate in them are highly preferred deer food. This could potentially result in the loss of a forest cover. Forests on poor soils (M types), although often containing many highly preferred species (e.g., MI in Milford/Bligh Sound), are less susceptible due to the abundance of many unpreferred species that could replace preferred plants.

Acknowledgements

The authors acknowledge assistance from numerous summer field staff for data collection, especially R. Morison who led the field party. We also thank J. von Tunzelmann and the staff of the New Zealand Forest Service, Te Anau, for logistic support. A. Rose made helpful comments on an early draft of the manuscript and J. Orwin provided invaluable editorial assistance.

References

- Allan, H.H. 1961. *Flora of New Zealand*. Volume 1. Government Printer, Wellington.
- Allen, R.B.; McLennan, M.J. 1983. *Indigenous forest survey manual: two inventory methods*. New Zealand Forest Service, FRI Bulletin No. 48: 73pp
- Edgar, E. 1973. Names in *Pseudopanax* C. Koch (Araliaceae). *New Zealand Journal of Botany* 11: 171-172.
- Holloway, J.T. 1950. Deer and the forests of western Southland. *New Zealand Journal of Forestry* 6: 123-137.
- Mark, A.F.; Baylis, G.T.S. 1975. Impact of deer on Secretary Island, Fiordland, New Zealand. *Proceedings of the New Zealand Ecological Society* 22: 19-24.
- Mason, R. 1951. Deer and the vegetation (b) deer stomach contents. In: A.L. Poole (Compiler). *Preliminary reports of the New Zealand-American Fiordland Expedition. Investigations in Fiordland, New Zealand, in 1949*. pp. 29-31. New Zealand Department of Scientific and Industrial Research Bulletin 103.
- Moore, L.B.; Edgar, E. 1970. *Flora of New Zealand*. Volume 2. Government Printer, Wellington.
- Nugent, G.; Parkes, J.P.; Tustin, K. 1987. Changes in the density and distribution of red deer and wapiti in northern Fiordland. *New Zealand Journal of Ecology* 10 (this volume).
- Rose, A.B.; Burrows, I.E. 1985. The impact of ungulates on the vegetation. In: Davis, M.R.; Orwin, J. (Editors). *Report on a survey of the proposed Wapiti area, West Nelson*. pp. 210-234. New Zealand Forest Service, FRI Bulletin No. 84.
- Stewart, G.H.; Harrison, J.B.J. 1987. Physical influences on forest types and deer habitat, northern Fiordland, New Zealand. *New Zealand Journal of Ecology* 10 (this volume).
- Veblen, T.T.; Stewart, G.H. 1982. The effects of introduced wild animals on New Zealand forests. *Annals of the Association of American Geographers* 72: 372-397.
- Wardle, J.A. 1984. *The New Zealand beeches ecology, utilization and management*. New Zealand Forest Service, Christchurch, New Zealand. 447 pp.
- Wardle, J.; Hayward, J.; Herbert, J. 1971. Forests and scrublands of northern Fiordland. *New Zealand Journal of Forestry Science* 1: 80-115.
- Wardle, J.A.; Stewart, G.H. 1986. Permanent plot monitoring in forests. In: Stewart, G.H.; Orwin, J. (Collators and editors). *Indigenous vegetation surveys: methods and interpretation*. pp. 51-54. Forestry Research Centre, Christchurch. 67pp.