

Long-term (20 years) effect of  
artificial defoliation of  
mid-ribbed snow tussock,  
*Chionochloa pallens*, in the  
Murchison Mountains, Fiordland,  
New Zealand

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## CONTENTS

Abstract	5
1. Introduction	5
2. Objectives	6
3. Methods	6
3.1 Site description and experimental treatments	6
4. Results	7
4.1 Tiller number, length, and basal diameter	7
4.2 Biomass	7
4.3 Mineral nutrients	10
5. Discussion	10
5.1 Increasing size of tussocks in control plots	10
5.2 Changes in biomass and patterns of mineral nutrient allocation in both treatments	15
5.3 Rates of recovery following defoliation	16
6. Conclusions	17
7. Acknowledgments	17
8. References	17

# Abstract

Biomass, tillering, and mineral nutrient levels were measured in tussocks of *Chionochloa pallens* in low alpine grasslands in March 1998, 19.5 years after clipping and removal of green lamina material in spring 1977. Tussock features were compared between treatments (control or defoliated), and with a previous sampling in 1986. For all features defoliated tussocks showed continued convergence toward plants in control plots. Mineral nutrient concentrations, amounts per unit area, and allocation patterns within plants, showed few significant differences between control and defoliated treatments after 20 years. Similarly, biomass allocation to roots, stem, and leaves was not significantly different between treatments. However, tiller dry weights and size (length, basal diameter), and tussock dry weight per unit area remain significantly depressed in the defoliated plots (c. 30%) compared with control plots. While most tussock features, especially nutrient concentrations, appear to have recovered from a single severe defoliation in approximately two decades, tussock biomass (per tiller and per unit area) will take a further 5 years to reach levels comparable to the control tussocks, assuming minimal deer grazing.

## 1. Introduction

In 1977 an experimental investigation was begun into the effects of deer and takahe grazing on the mid-ribbed snow tussock, *Chionochloa pallens*, in the Murchison Mountains, Fiordland (Lee et al. 1988). *Chionochloa pallens* is restricted to high fertility soils associated with alluvial and colluvial systems in the alpine zone where it is favoured by both animals. Deer feed on the tussock leaf blades while takahe eat the basal leaf meristem and discard the lamina material. Deer and takahe both select the most nutritious plants available (Mills and Mark 1977, Mills et al. 1989, Mills et al. 1991).

To determine the long-term impact of deer on *C. pallens*, experimental plots were established in November 1977, involving the clipping of all tussocks at the leaf and sheath junction in five plots of 5 × 5 metres. This removed all mature green lamina material from the tussocks. Comparable control (unclipped) plots were established at the same time. Biomass, tillering, and plant chemistry (mineral nutrients and carbohydrates) were measured in both defoliated and control plots in April 1986, 8 years after the experiment was established. Results showed that defoliation had increased tiller density, and depressed tiller size and tussock biomass. Defoliation also decreased the proportion of total biomass and mineral nutrients allocated to roots. It was predicted that it would take at least two decades for the defoliated tussocks to recover from the clipping, even in the absence of deer grazing (Lee et al. 1988).

## 2. Objectives

To examine aspects of the response of *Chionochloa pallens* to simulated grazing nearly 20 years after the treatments were applied, by analysing in defoliated and control tussocks:

- tiller density,
- biomass,
- concentration of mineral nutrients,
- allocation of resources to different plant parts.

## 3. Methods

### 3.1 SITE DESCRIPTION AND EXPERIMENTAL TREATMENTS

A full description of the site and experimental treatments is given in Lee et al. (1988). An approximately 1 hectare area of *C. pallens* occupies gently sloping colluvial and alluvial deposits backed up behind a roche moutonnée at the mouth of the cirque basin at the eastern end of the Dana Peaks area, Murchison Mountains, Fiordland. Experimental plots were established in 1977 on the lower, more stable, parts of the grassland (Grid Reference D42 903 393).

In March 1998, 19.5 years after the tussocks were clipped, all *C. pallens* material was removed from a randomly located 0.5 × 0.5 m quadrat in each of the five replicate plots of defoliated and control treatments. The locations of quadrats sampled in April 1986 were marked with pegs, and these were intentionally avoided in the current sampling.

*Chionochloa pallens* plants, including roots to a depth of 100 mm, were collected. After washing and the removal of attached dead sheaths, stem, and root material, the basal diameter (mm) and the length (cm) of the longest leaf was measured for all tillers, and the plant material partitioned into the following fractions:

- attached dead leaf sheaths;
- brown dead leaf blade tips—distal dieback section;
- green leaf blades—all green material above the sheath / blade junction of the outermost functional leaf;
- differentiated sheath—all material below the sheath / blade junction of the outermost functional leaf;
- stem;
- roots—mainly living material.

All plant material fractions were washed in distilled water and oven dried at 60°C for several days until constant weight was achieved. Using a Cyclone sample mill, dried plant material was ground to pass through a 1-mm screen, and mineral nutrient levels were determined following methods in Blakemore et al. (1987).

Where necessary, raw data were transformed to normalise distributions. Treatment, year, and interaction effects were examined using repeated measures ANOVA. Statistical analyses were undertaken using the package TEDDYBEAR (Wilson 1991).

## 4. Results

### 4.1 TILLER NUMBER, LENGTH, AND BASAL DIAMETER

Results for mean tiller number, length, and diameter in treatments in 1986 and 1998 are presented in Table 1, with size range classes for tillers shown in Figure 1.

Tiller density in control plots was similar in 1998 to that found earlier, although the tillers were on average 10% longer (c. 5 cm) and wider (c. 0.8 mm) than in 1986 (Table 1, Fig. 1). The density of defoliated tillers shows a decline since 1986 and is currently similar to that found in the control plots (i.e. c. 120 per 0.25 m<sup>2</sup>). Mean tiller diameter and length of defoliated tillers also increased significantly since 1986, by at least 50%, as shown in the marked shift of modal values in Figure 1. However, both tiller length and basal diameter in defoliated plots in 1998 were significantly lower (20% less) than those in control plots.

### 4.2 BIOMASS

Biomass values on a tiller, per unit area, and allocation basis are presented in Table 2.

TABLE 1. TILLER FEATURES OF CONTROL (C) AND DEFOLIATED (D) *Chionochloa pallens*, FIORDLAND, 8 (1986) AND 20 (1998) YEARS AFTER TREATMENTS WERE ESTABLISHED.

				STATISTICAL SIGNIFICANCE		
	TREATMENT	1986	1998	Tr	Yr	In
Tiller number	C	120	120	NS	NS	NS
	D	179	143			
Tiller diameter (mm)	C	5.8	6.7	***	***	NS
	D	3.5	5.3			
Tiller lengths (cm)	C	49.6	55.0	***	**	NS
	D	26.1	43.7			

Statistical significance is as follows: \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001, NS not significant. Tr = treatment; Yr = year; In = treatment-year interaction. Values are means of five replicates.

Figure 1. Size frequency distribution for length and basal diameter of control and defoliated tillers of *Chionochloa pallens*, Fiordland, sampled in 1986 (white) and 1998 (black).

TABLE 2. DRY WEIGHT FEATURES OF CONTROL (C) AND DEFOLIATED (D) *Chionochloa pallens*, FIORDLAF AFTER TREATMENTS WERE ESTABLISHED.

TREATMENT	DRY WEIGHT PER TILLER (mg)				DRY WEIGHT PER (0.5 × 0.5 m) AREA (g)				
	1986	1998	Tr	Yr	1986	1998	Tr	Yr	1986
<b>Live Plant</b>									
Greenblade	C	575	843	***	**	NS	**	NS	13.4
	D	153	519					NS	16.5
Sheath	C	436	578	***	*	NS	**	NS	10.6
	D	129	359					NS	13.4
Stem	C	695	276	***	*	**	**	*	16.2
	D	136	174					NS	14.6
Roots	C	1363	1022	*	NS	*	*	NS	30.5
	D	250	906					NS	25.0
<b>Dead Plant</b>									
Leaf tip	C	133	100	***	NS	NS	*	NS	3.2
	D	56	68					NS	6.2
Attached sheath	C	1131	1932	**	**	NS	**	*	25.2
	D	229	1326					NS	24.4
<b>Total Biomass</b>	C	4333	4751	**	*	NS	**	NS	NS
	D	953	3351					NS	NS

Statistical significance is as follows: P<0.001\*\*\*; P<0.01>0.001\*\*; P<0.05>0.01\*; P>0.05 non-significant NS. Tr = t year interaction. Values are means of five replicates.



In 1998 mean dry weight of tillers in the control plots was 4.75 g or 580 g per 0.25 m<sup>2</sup>, representing a 10% increase over 1986 values. In the defoliated plots, tiller dry weight and biomass per unit area were both approximately 70% of the controls in 1998, up from 22% and 37% respectively in 1986. Values for individual tiller components (e.g. green blade, sheath) generally increased in both treatments over the sampling interval, with the defoliated plots converging to within 30% of control plots. Currently, tiller dry weights and the dry weight of *C. pallens* per unit area are significantly lower in defoliated plots than in the control plots. A striking difference is the large increase (>70%) in attached dead sheath material across both treatments, and the decrease in stem material (mainly in control plots) from 1986 to 1998. This is reflected in biomass allocation patterns, with the stem fraction declining from c. 13% of total biomass in both treatments in 1986, to form less than 6% in 1998. Attached sheath material, in contrast, increased from c. 22% in 1986 to over 35% in 1998.

#### 4.3 MINERAL NUTRIENTS

Mineral nutrient concentrations, amount per unit area, and allocation patterns are presented for defoliated and control plots in Tables 3a, 3b, 4a, 4b, and 4c.

Overall, most mineral nutrient concentrations show no treatment or year effects. Calcium, and to a lesser extent magnesium, potassium (mostly with significantly lower concentrations in 1998), and sodium (significantly higher concentrations in 1998), showed significant year effects for at least three tiller fractions. Roots (N, P, K, Ca, Mg) and dead leaf tips (P, K, Ca, Mg, Na) showed consistent decreases in concentrations of most mineral elements between 1986 and 1998 samplings. Treatment effects are few (6 out of a possible 36) and mostly indicate a lower concentration in defoliated tissues (N—green blade; K—roots; Mg—stem; Na—green blade and leaf tip).

Allocation patterns (Tables, 4a, 4b, 4c) for total mineral nutrients showed strong year effects for all mineral elements, with an increasing proportion of nutrients in green blade, sheath, and attached sheath, and a decreasing proportion in stem, root, and dead leaf tip components. However, there were very few significant treatment effects.

## 5. Discussion

### 5.1 INCREASING SIZE OF TUSSOCKS IN CONTROL PLOTS

In 1998 *Chionochloa pallens* tussocks in the control plots showed an increase in tiller basal diameter (0.84 mm) and length (5.38 cm) compared with 1986 (Table 1). Some swelling of the basal portion of the tillers could have been expected following floral induction earlier in the summer (December-January)

TABLE 3a. MINERAL NUTRIENT (N, P, K) CONCENTRATIONS (mg/g DRY WEIGHT) OF CONTROL (C) AND *pallens*, FJORDLAND, 8 (1986) AND 20 (1998) YEARS AFTER TREATMENTS WERE ESTABLISHED.

TREATMENT	NITROGEN (N)				PHOSPHORUS (P)				CONCENT	
	CONCENTRATION		STATISTICAL SIGNIFICANCE		CONCENTRATION		STATISTICAL SIGNIFICANCE			
	1986	1998	Tr	Yr	In	1986	1998	Tr	Yr	In
<b>Live Plant</b>										
Greenblade	C	9.28	9.92	*	NS	NS	1.58	1.62	NS	NS
	D	8.44	7.76				1.78	1.42		
Sheath	C	7.02	6.78	NS	NS	NS	1.60	1.98	NS	NS
	D	8.14	7.54				1.80	1.76		
Stem	C	4.00	3.64	NS	NS	NS	0.64	0.76	NS	NS
	D	4.80	3.76				0.68	0.60		
Roots	C	6.28	4.44	NS	***	NS	1.12	0.72	NS	***
	D	6.30	4.66				1.00	0.62		
<b>Dead Plant</b>										
Leaf tip	C	4.52	4.52	NS	NS	NS	0.96	0.80	NS	***
	D	4.74	3.94				1.32	0.70		
Attached sheath	C	3.00	4.12	NS	*	NS	0.38	0.74	NS	NS
	D	3.42	4.6				0.44	0.84		

Statistical significance is as follows: P<0.001\*\*\*; P<0.01>0.001\*\*; P<0.05>0.01\*; P>0.05 non-significant NS. Tr = treatment-year interaction. Values are means of five replicates.

TABLE 3b. MINERAL NUTRIENT (Ca, Mg, Na) CONCENTRATIONS (mg/g DRY WEIGHT) OF CONTROL (C) A *pallens*, FIORDLAND, 8 (1986) AND 20 (1998) YEARS AFTER TREATMENTS WERE ESTABLISHED.

TREATMENT	CALCIUM (Ca)				MAGNESIUM (Mg)				CONCENT	
	1986	1998	Tr	Yr	1986	1998	Tr	Yr		In
<b>Live Plant</b>										
Greenblade	C	1.06	0.78	NS	*	NS		NS	NS	0.42
	D	0.84	0.58							1.06
Sheath	C	0.46	0.32	NS	*	NS		NS	NS	0.76
	D	0.48	0.26							1.72
Stem	C	0.56	0.24	NS	***	NS		*	*	0.48
	D	0.58	0.22							0.80
Roots	C	3.12	0.32	NS	***	NS		**	NS	0.50
	D	1.84	0.34							0.48
<b>Dead Plant</b>										
Leaf tip	C	2.12	1.10	NS	***	NS		**	NS	0.34
	D	2.04	0.84							0.66
Attached sheath	C	1.10	0.40	NS	***	NS		NS	*	0.24
	D	1.02	0.40							0.28

Statistical significance is as follows:  $P < 0.001^{***}$ ,  $P < 0.01 > 0.001^{**}$ ,  $P < 0.05 > 0.01^{*}$ ,  $P > 0.05$  non-significant NS. Tr = t year interaction. Values are means of five replicates.

TABLE 4a. ALLOCATION (%) OF MINERAL NUTRIENTS (N, P, K) WITHIN CONTROL (C) AND DEFOLIATED (D) TREATMENTS IN 1986 AND 1998 AT FJORDLAND, 8 (1986) AND 20 (1998) YEARS AFTER TREATMENTS WERE ESTABLISHED.

TREATMENT	NITROGEN (N)					PHOSPHORUS (P)					
	% ALLOCATION		STATISTICAL SIGNIFICANCE			% ALLOCATION		STATISTICAL SIGNIFICANCE			
	1986	1998	Tr	Yr	In	1986	1998	Tr	Yr	In	
<b>Live Plant</b>											
Greenblade	C	22.7	32.2	NS	NS	22.2	29.0	NS	NS	NS	30.7
	D	21.4	24.7			27.2	26.4				34.6
Sheath	C	13.1	15.1	NS	NS	17.0	22.0	NS	NS	NS	28.3
	D	16.4	15.7			22.3	21.2				31.5
Stem	C	11.9	3.72	NS	***	10.9	4.3	NS	***	NS	10.3
	D	10.5	3.38			9.0	3.2				7.7
Roots	C	35.1	18.1	NS	*	36.0	15.7	NS	**	*	21.7
	D	24.6	24.3			23.8	18.7				14.1
<b>Dead Plant</b>											
Leaf tip	C	2.6	1.8	NS	***	3.2	1.9	*	****	**	3.6
	D	4.5	1.6			7.6	1.6				6.6
Attached sheath	C	14.6	29.0	NS	***	10.7	27.2	NS	**	NS	5.5
	D	13.0	30.3			10.1	29.0				5.5

Statistical significance is as follows:  $P < 0.001$ \*\*\*,  $P < 0.01 > 0.001$ \*\*\*,  $P < 0.05 > 0.01$ \*;  $P > 0.05 > 0.01$ \*;  $P > 0.05 > 0.01$ \*;  $P > 0.05 > 0.01$ \* non-significant NS. Tr = 1 year interaction. Values are means of five replicates.

TABLE 4b. ALLOCATION (%) OF MINERAL NUTRIENTS (Ca, Mg, Na) WITHIN CONTROL (C) AND DEFOLIA' FIORDLAND, 8 (1986) AND 20 (1998) YEARS AFTER TREATMENTS WERE ESTABLISHED.

TREATMENT	CALCIUM (Ca)				MAGNESIUM (Mg)				% ALLOC 1986	
	% ALLOCATION		STATISTICAL SIGNIFICANCE		% ALLOCATION		STATISTICAL SIGNIFICANCE			
	1986	1998	Tr	Yr	In	1986	1998	Tr	Yr	In
<b>Live Plant</b>										
Greenblade	C	9.6	30.9	NS	**	NS	34.5	NS	**	*
	D	12.5	25.2			NS	27.4			
Sheath	C	3.14	8.4	NS	**	NS	11.6	NS	NS	*
	D	5.54	7.5			NS	10.2			
Stem	C	5.8	2.8	NS	***	NS	3.3	NS	***	*
	D	7.7	2.5			NS	2.5			
Roots	C	57.0	17.0	NS	***	*	17.9	NS	**	*
	D	40.8	24.6			NS	21.9			
<b>Dead Plant</b>										
Leaf tip	C	4.3	5.4	*	**	***	3.0	*	***	***
	D	11.2	4.9			***	2.3			
Attached sheath	C	20.1	35.4	NS	*	NS	29.8	NS	***	NS
	D	22.2	35.4			NS	35.6			

Statistical significance is as follows: P<0.001\*\*\*; P<0.01>0.001\*\*; P<0.05>0.01\*; P>0.05 non-significant NS. Tr = t year interaction. Values are means of five replicates.

when mean daily temperatures exceeded the temperature threshold required to induce a mast flowering. However, the previous sampling in 1986 was similarly associated with the initiation of mast flowering. It is likely that the increasing size of the tillers in the control plots reflects both the low levels of deer grazing in the basin over the last decade, and the absence of site disturbance, particularly inundation and deposition of fresh colluvial or alluvial material, as is typical of *C. pallens* sites in other parts of the cirque basin.

## 5.2 CHANGES IN BIOMASS AND PATTERNS OF MINERAL NUTRIENT ALLOCATION IN BOTH TREATMENTS

In both defoliated and control treatments there was a significant change in the proportion of sheath, dead leaf tip (increase), and stem (decrease) between the two harvests. This is unlikely to have been caused by differences in identifying plant portions at the time of the two samplings, especially for the attached sheath and dead leaf tip. Comparison of flowering frequency and intensity between the two sampling intervals (1977-1986, 1986-1998), based on the long-term flowering transect nearby in Takahe Valley, Murchison Mountains, shows no discernable difference that would account for major changes in vegetative allocation patterns. The proportion of dead leaf tip on the tussocks in Fiordland varies seasonally (Mills et al. 1991), and differences between years may merely reflect local conditions during the recent growing season. The increase in sheath material between 1986 and 1998 may indicate long-term site

TABLE 4c. ALLOCATION (%) OF TOTAL MINERAL NUTRIENTS WITHIN CONTROL (C) AND DEFOLIATED (D) *Chionochloa pallens*, FIORDLAND, 8 (1986) AND 20 (1998) YEARS AFTER TREATMENTS WERE ESTABLISHED.

TREATMENT		TOTAL MINERAL NUTRIENTS				
		% ALLOCATION		STATISTICAL SIGNIFICANCE		
		1986	1998	Tr	Yr	In
<b>Live Plant</b>						
Greenblade	C	19.0	30.5	NS	**	*
	D	23.4	27.4			
Sheath	C	14.1	20.3	NS	***	**
	D	18.9	19.5			
Stem	C	10.3	5.4	NS	***	NS
	D	9.6	4.1			
Roots	C	40.3	16.5	NS	***	**
	D	27.0	20.5			
<b>Dead Plant</b>						
Leaf tip	C	3.3	2.4	*	***	***
	D	7.4	2.1			
Attached sheath	C	13.1	25.1	NS	***	NS
	D	12.2	26.2			

Statistical significance is as follows: \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001, NS not significant. Tr = treatment; Yr = year; In = treatment-year interaction. Values are means of five replicates.

stability, as the material would be readily removed if the area received fresh colluvial or alluvial material. The significant decline in the proportion of stem is unexplained.

Calcium concentrations in all plant tissues showed a significant decline in 1998, most likely because of increasing soil maturity in the absence of fresh parent material on the site. However, soil pH (c. 5.0) remained constant between samplings, and there were no significant changes in other soil nutrients. Allocation patterns for mineral nutrients differed between samplings for all plant parts (Table 4). Based on mineral nutrient totals, there was a significant increase in the proportion allocated to above-ground components (e.g. green blade, sheath, and attached sheath), and a significant decrease in amounts found in below-ground parts (e.g. stem, roots).

### 5.3 RATES OF RECOVERY FOLLOWING DEFOLIATION

In the first summer following clipping of the tussocks, a pair of takahe preferentially fed on the cut tillers, removing approximately 10% of the total available. Since then a pair of takahe have intermittently occupied the basin, and deer grazing has been minimal. The recovery of the defoliated *C. pallens* plants has continued from 1986 to 1998, and there are currently few significant differences with respect to tiller number, biomass allocation, and mineral nutrient profile between cut and control tussocks. These improvements in the defoliated tussocks suggest that levels of herbivory over the last decade have not impeded tussock growth and recovery.

However, the 1998 assessment detected some significant differences between tussocks in defoliated and control plots, even after nearly 20 years. Defoliated plot tillers are on average smaller and the amount of tussock biomass per unit area lower, compared with tussocks in control plots. Defoliation initiated massive tillering in the first few seasons, resulting in a 50% increase in tiller density in 1986, 8 years after the clipping. In the recent sampling, tiller densities are similar in both treatments, presumably due to higher tiller mortality, perhaps of the original cut tillers, in the defoliated plots. The new cohort of tillers in these plots is still evident in the basal diameter and tiller length profiles. Assuming a linear recovery rate comparable to what has occurred between sampling in 1986–1998, *C. pallens* biomass in defoliated plots should match that of the controls in a further 5 years (i.e. by 2003).

*Chionochloa pallens* has one of the fastest relative growth rates of any *Chionochloa* species in Fiordland (Mills et al. 1991) and would be expected to show the most rapid rate of recovery after clipping, especially when growing on fertile soils. Thus the time taken for *C. pallens* to recover (25 years) is likely to be less than that for most other *Chionochloa* species.

## 6. Conclusions

Resampling of *C. pallens* plots established in 1977 showed that while tiller density and nutrient profiles of tussocks had recovered from a single severe defoliation, tiller weights and size, and the amount of tussock per unit area, remain significantly depressed and are approximately 70% of values of those of control tussocks. Recovery of the dominant *Chionochloa* grasses in Fiordland after high deer numbers in the alpine zone during the 1950s and 1960s is likely to take a minimum of several decades, and much longer for those elements of the local flora that were largely eaten out of many communities.

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