Chapter 3:

Upland plant responses to simulated seasonal herbivory

3.0 SUMMARY

A cutting experiment was carried out to determine the effect of seasonal herbivory on upland plant species belonging to different communities – grasslands and mires. Five treatments were applied: control (uncut); cut in July 2000 and July 2001; cut in October 2000; cut in March 2001; cut in May 2001 and July 2001. These treatments allowed the impact of season of herbivory and length of regrowth to be assessed. After each cut, individual plants of several species were marked and their height measured at intervals through the growing season. The results were related to plant growth form. The majority of species in the grassland communities were wintergreen graminoids, and these showed relatively little variation in response to cutting in different seasons. In mire communities, the species belonged to a variety of growth forms, including wintergreen and non-wintergreen, graminoids and dwarf shrubs. There was greater between-species variation in length of time taken to grow 5 cm following cutting in mire communities than in grassland communities.

3.1 INTRODUCTION

Knowledge of plant responses to tissue loss is a powerful tool to aid understanding of changes in species abundance in grazed systems (section 6.1). Upland plants have a range of life forms and phenologies (Table 3.1), from evergreen grasses to deciduous dwarf shrubs and forbs. Plant life-form and phenology (Archer & Tieszen, 1985; Grime, 2001), the season of herbivory (Augustine & McNaughton, 1998), and the interval between herbivory events (Ferraro & Oesterheld, 2002) are thought to interact to affect species relative performance.

The ability of plant species to tolerate grazing depends largely on the ready availability of meristematic areas that can replace lost tissue rapidly (Richards, 1993). Different growth forms have different potential for this (Archer & Tieszen, 1980), and because of the seasonal developmental pattern of species, their ability to re-grow also varies with season of cutting (Wells, 1971). Graminoids extend their leaves from the base, meaning that herbivory is unlikely to remove vegetative meristems (Archer & Tieszen, 1985). Dwarf shrubs, at the opposite extreme, have their meristematic material at or near the shoot tips, making them vulnerable to grazing. The impact of the seasonal timing of a herbivory event is influenced by whether the species is capable of growth during that season, and whether the plant has reserves available for re-growth at that time. Floate *et al.* (1979) group upland species into three types: 1. evergreen and capable of growing whenever temperature and light conditions are suitable (most of the upland acid grassland species lie within this category); 2. evergreen but can only grow at one time of the year (e.g. evergreen dwarf shrubs); 3. deciduous plants. Grime (2001) proposes that the life-form strategies that have evolved in infertile habitats tend to be evergreen since this conserves resources.

Table 3.1. Species in the cutting experiment and their characteristics.

	Gross Morph[1]	Veg Persistence[2]	Height[3]	Flowering Time[4]	Growth Pattern[5]	Tussocks/ Tufted[6]
Grassland Species						
Agrostis capillaris	G	Rhizomes	70	6-8	EA	Tu
Anthoxanthum odoratum	G	?	50	4-6	EA	Tu
Carex binervis	G	Rhizomes	150	6-6	EA	Tu
Carex panicea	G	Rhizomes	40	6-7	EA	Tu
Festuca ovina	G	Rooting stems	60	6-8	EA	Tu
Galium saxatile	F	Rooting Stems	20	6-8	EA	N
Nardus stricta	G	Rhizomes	40	6-8	EA	T
Potentilla erecta	F	Basal stock	30	6-9	Sa	N
Vaccinium myrtillus	S	Rhizomes	60	4-6	Sa	N
Mire Species						
Calluna vulgaris	S	Rooting stems	60	7-9	E	N
Erica tetralix	S	Rhizomes	60	6-9	E	N
Eriophorum angustifolium	G	Rhizomes	60	3-6	E	Tu
Eriophorum vaginatum	G	Rhizomes	60	3-5	E	T
Molinia caerulea	G	Rhizomes	150	6-8	Sa	T
Narthecium ossifragum	G	Rhizomes	45	7-9	Sa	Tu
Trichophorum cespitosum	G	Rhizomes	35	5-6	Sa	T

[1] Gross Morphology: plants classified by author into 3 categories: G = Graminoid (plant with grass-like form – linear leaves, leaf extension from base; F = Forb (non-woody plant with branched form); S = Shrub (woody plant). [2] Method of vegetative persistence, from Ecoflora database Fitter & Peat (1994); Clapham, Tutin & Moore (1987) and Stace (1991). [3] Typical Maximum height, also from Ecoflora database and Stace (1991). [4] Normal earliest month of flowering – Normal latest month, from Ecoflora database (Fitter & Peat, 1994; www.york.ac.uk/res/ecoflora/cfm/ecofl/index.cfm). [5] Growth pattern: EA = Evergreen, capable of growth year round if temperatures suitable, E = Evergreen, but only capable of growth at certain times of the year, E(s) = sometimes evergreen, Sa = Seasonal aestival (growth spring-autumn, leaves die back over winter). [6] Tussock forming: N = not tussock forming; not tufted, Tu = tufted, T = tussocks (author's knowledge).

A field-based cutting experiment was carried out to increase understanding of the effects of seasonal grazing regimes on different plant life-forms and to generate information for the modelling chapter (section 6.3.3b.). This approach was adopted since it gave an ecologically relevant growth environment (which a glass-house experiment would not have done) but still allowed control of the timing of tissue removal (which observations of sheep grazing would not have done). There are questions over the appropriateness of simulating herbivory rather than using real herbivory (Baldwin, 1990), but it was felt in this case to give the most useful information in the time available.

3.2 OBJECTIVES

Objective: Provide information on the effects of seasonal herbivory on upland plant species with a range of life-forms and phenologies.

Sub-objectives:

1. Determine the effect of cutting in different seasons on relative plant performance.
2. Determine the effect of different lengths of recovery time on relative plant performance.

3.3 METHODS

The experimental period was May 2000 to October 2001. The work was carried out *in situ*, in an area of Kirkton Glen from which herbivores had been excluded since winter 1998 (Section 2.2.3).

3.3.1 Sampling areas

Four sampling areas (Table 3.2; Fig 3.1) were set up in April 2000, two on upland *Nardus* grassland communities and two on mire communities. Each sampling area was approximately 50 m by 50 m in size. Within each sampling area, five 20 m transects with random start points and running along random compass bearings were set up; some of the transect lines therefore crossed. In spring 2000, thirty 40 cm by 40 cm quadrats were established using short bamboo canes to mark three of the corners of each quadrat. The quadrats were positioned at five random distances along each transect, with alternate quadrats to the left and right side of the transect. In the grassland communities, if the random quadrat fell within a flush, it was progressively re-positioned 1 m further along until it was on representative ground.

Table 3.2. Altitude and NVC community of sampling areas.

Site	Altitude (m)	NVC Community (Rodwell, 1991; 1992)	Description
A	450	U5	Upland *Nardus stricta-Galium saxatile* grassland, gently sloping
B	520	U5/CG11	Mosaic of U5 and calcicolous *Festuca ovina-Agrostis capillaris-Alchemilla alpina* grass-heath, moderately steep ground
C	430	M15/M17	*Trichophorum caesptosum-Erica tetralix* wet heath / *Trichophorum caespitosum-Eriophorum vaginatum* blanket mire, *Molinia* dominated, flat ground
D	470	M15/M17	*Trichophorum caesptosum-Erica tetralix* wet heath / *Trichophorum caespitosum-Eriophorum vaginatum* blanket mire, *Trichophorum* dominated, flat/undulating ground

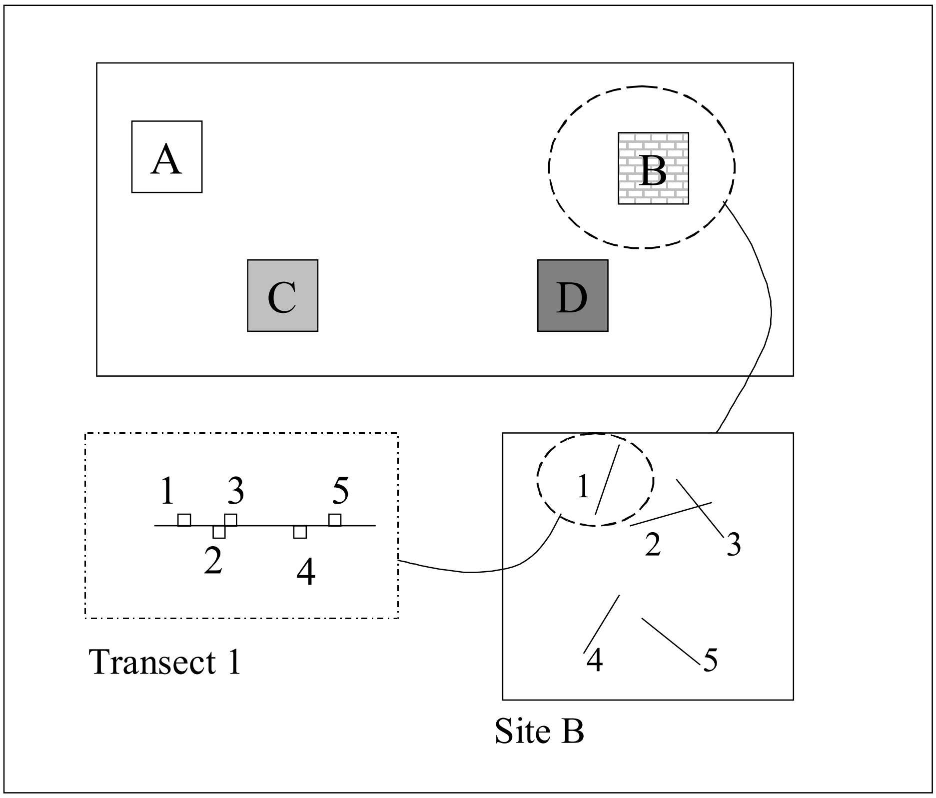

Fig 3.1. Schematic diagram of layout of sampling areas A-D. Random position of transects in sites and quadrats along transects are shown. A = white, B = bricks, C = light grey, D = dark grey.

3.3.2 Treatments

Five treatments (Table 3.3) were allocated at random to the quadrats in the sampling areas as a whole, with transects used only to facilitate quadrat relocation. Two of the treatments involved cutting quadrats only once in October 2000 or March 2001. Two treatments involved two cuts, either in the same year (May and July 2001) or in different years (July 2000 and 2001). The control quadrats were never cut. The vegetation in the entire quadrat, and any vegetation hanging over the quadrat, was cut using gardener's hand shears. A 6 cm block was used as a guide to ensure the overall height of the cut was consistent. Leaves of herbs were lifted before cutting so that individuals were cut to 6 cm. Dwarf shrubs were cut without lifting stems, resulting in a smaller proportion of the plant being removed, as a cut 6 cm from the base of dwarf shrubs would have removed all green material and cut into the woody stem.

Table 3.3. Treatments applied. All quadrats in the treatment were cut within 1 week of the date given, except where stated.

Treatment name	**1st Cut**	**2nd Cut**
Control	-	-
July 2000 & 2001* (long-recovery)	27th June 2000	10th July 2001
October 2000	16th October 2000	-
March 2001	15th - 29th March 2001	-
May & July 2001 (short-recovery)	8th May 2001	10th July 2001

3.3.3 Measurements

Selection and marking of individuals / tillers

Individuals for measurement were selected haphazardly following cutting (or in July 2000 for controls). One individual (herbs and dwarf shrubs) or one tiller (graminoids) of each of the species of interest (Table 3.1) was marked by loosely wrapping a coloured wire around the base. Not all species occurred in all quadrats, making the sample sizes unbalanced (Table 3.4). As the experiment progressed, the control plants and those cut early in the experiment became increasingly difficult to find, so they were marked using a white gardener's plant tag and a piece of wire. There was no overlap in species selected between the grassland and mire sites.

Height measurements

A quick, non-destructive measurement was required to chart the progress of plants. Other studies of responses to herbivory commonly use the production of above-ground biomass as a response variable (e.g. Grant *et al.* 1996 a, Grant *et al.* 1996 b). In this study, height of leaves / shoots was selected, since it is applicable to a range of life forms, is non-destructive and reasonably quick to carry out (all marked plants could be surveyed in 3 days, including travelling time). Average length of the three longest live leaves was selected as the most appropriate parameter for graminoids (Poaceae, Cyperaceae), and total length of shoot for dwarf shrubs and forbs. Graminoids were recorded by holding in turn the three longest living leaves against a clear plastic ruler, measuring each from ground level to leaf tip. 'Live' was defined as 'having some green material'. Growth rates can therefore be positive (when the measured leaves were increasing in length), zero, or negative (when the previously longest leaf died and was replaced in measurement by a shorter one). Forbs were recorded by measuring from ground level to the single highest shoot tip. Measurements of dwarf shrubs were found to give variable results when measured from ground level to shoot tip, so they were marked on the woody stem with a spot of blue acrylic paint, and the shoot length measured from this point to the highest tip. In the cut treatments, height measurements were made immediately after cutting, and at approximately four-weekly intervals during the following growing seasons, until October 2001. Data were collected only once between November and February inclusive, due to snow cover. Control plants were measured from July 2000 onwards.

Table 3.4. Sample sizes of species in site × treatment combinations. If individuals had died, been grazed or lost their tag, the numbers measured in the second cuts of the repeat cut treatments decreased. In some instances, new individuals were marked in the second cut, increasing the sample size.

		Treatment name and cut number						
		July 00 & 01		Oct 00	Mar 01	May &July 01		Control
	Site	1	2	1	1	1	2	
Grassland Species								
Agrostis capillaris	A	4	3	3	6	5	5	4
Agrostis capillaris	B	5	5	5	3	3	3	5
Anthoxanthum odoratum	A	1	2	2	1	1	1	1
Anthoxanthum odoratum	B	1	1	1	3	3	3	0
Carex binervis	A	0	0	1	0	2	3	0
Carex binervis	B	2	2	5	3	5	5	1
Carex panicea	A	4	3	5	3	5	3	6
Carex panicea	B	3	5	0	0	0	0	2
Festuca ovina	A	6	5	4	6	4	6	4
Festuca ovina	B	6	4	5	5	5	5	5
Galium saxatile	A	6	1	2	3	2	1	1
Galium saxatile	B	6	2	2	4	5	4	0
Nardus stricta	A	6	5	4	6	5	6	2
Nardus stricta	B	6	5	5	6	5	5	6
Potentilla erecta	A	5	2	1	0	0	1	2
Potentilla erecta	B	6	0	4	2	1	2	0
Vaccinium myrtillus	A	5	2	0	2	2	6	3
Vaccinium myrtillus	B	6	2	4	5	5	5	6
Mire Species								
Calluna vulgaris	C	4	3	5	5	2	2	5
Calluna vulgaris	D	3	2	5	4	4	2	3
Erica tetralix	C	4	4	4	2	3	3	3
Erica tetralix	D	5	3	5	6	4	4	6
Eriophorum angustifolium	C	5	5	6	6	6	5	4
Eriophorum angustifolium	D	6	6	4	6	6	6	5
Eriophorum vaginatum	C	3	2	6	6	4	5	3
Eriophorum vaginatum	D	5	4	5	6	6	5	4
Molinia caerulea	C	1	1	2	1	3	4	1
Molinia caerulea	D	4	3	3	4	5	4	5
Narthecium ossifragum	C	5	5	5	2	2	6	3
Narthecium ossifragum	D	6	3	6	6	3	5	5
Trichophorum cespitosum	C	5	5	5	4	5	6	5
Trichophorum cespitosum	D	6	5	6	6	5	5	6

3.3.4 Data management and analysis

Data management

A total of 830 individual plants were recorded repeatedly. The data relating to each measurement on each plant were stored in an Access database. For the cut treatments, the database stored information on the number of weeks since cutting. For the control treatment, information on the number of weeks since estimated mean air temperature exceeded 6 $^{\circ}$C was stored. Estimated mean air temperature was determined using data from the nearest weather recording station (250-350 m below the study site), assuming a lapse rate of 6 $^{\circ}$C km^{-1}. Estimated mean air temperature exceeded 6 $^{\circ}$C in calendar week 19 (around 8th of May) in both years.

Before analysis, the three measurements of the graminoids were averaged to give a single height, and the woody plant heights were corrected by the height of the mark on their stem. Sixteen individuals had been grazed during the experimental period. Any measurements collected on these plants on or after the date that evidence of grazing was observed were excluded from the analysis. Several individuals died during the experiment; the proportion of the total that these represent was calculated, and they were included in the analysis described below.

Data analysis: time taken to reach 5 cm

The time taken by individuals to grow by 5 cm was selected as an appropriate response variable by which to compare treatments and the performance of species. Graphs of change in height against change in time were plotted for each species × treatment × cut number combination. For cut treatments, the x-axis was the number of weeks since cutting. Graphs of each of the control individuals for 2001 were plotted, using the number of weeks since degree days became positive for the x-axis. A horizontal reference line at 5 cm was plotted, and the number of weeks taken by each individual to grow 5 cm was noted. Some individuals never achieved 5 cm growth; these were assigned an arbitrary classification of ’54 weeks’ (longer than the experimental period). To compare treatments, plants that did not grow by 5 cm were excluded, treatment averages and standard deviations were calculated.

The proportion of plants achieving 5 cm growth was calculated as a total of all plants. Average values of weeks to reach 5 cm were calculated for each species × treatment combination, using all values including the '54's that had never achieved 5 cm. Three species with less than 30 individuals were excluded from the calculation of ranks: *Anthoxanthum odoratum*, *Carex binervis* and *Potentilla erecta*. The average values for time to 5 cm were then ranked, with the species with the fastest average time to grow 5 cm ranked '1'. Use of the data on the ordinal scale was selected since it is the type of information needed for the modelling work (section 6.3.3b), and also allows straightforward interpretation of this complicated data-set. Including values assigned as an arbitrary classification in the calculation of the mean is not statistically valid. It was carried out here to allow the fact that many plants failed to grow by 5 cm to influence the results.

Further analyses were considered:

- fitting curves to the growth of each of the individuals, followed by a test for treatment effect of the parameters of the curves using a variance components model (REML), since the data are unbalanced. The model used would have been growth rate = treatment × site (fixed factors) with the random term unspecified.
- carrying out a test for treatment effect on the final heights of individuals in August, using a variance components model. However, since the species have innately different heights, separate analyses would have been necessary for each species (I. Nevison, BIOSS, pers. com.), giving a high likelihood of a Type II error occurring. Since the rank data gave sufficient results, the further analyses described were not carried out.

If there was an opportunity to re-run the experiment, larger quadrats would be used to ensure that all of the species lay within most quadrats. This would allow a more simple statistical analysis, based on ANOVA, to be carried out.

3.4 RESULTS

3.4.1 Individual / tiller death

Survival of individuals and tillers varied between species, but was generally high (Table 3.5.). Of the mire species, the dwarf shrubs were worst affected, with low proportions of individuals of the other species dying. Records of deaths are biased against the grassland forbs, as they have a long flowering stem that died at the end of the growing season, and, in general, new shoots of the same individual were not marked at the start of the following growing season. Some tillers of the grasses *Agrostis capillaris* and *Anthoxanthum odoratum* died, but there were no deaths of *Festuca ovina* or *Nardus stricta* tillers. When the proportions of dead individuals are broken down by site and treatment, it can be seen that there is an interaction, with many individuals of *Calluna vulgaris* dying at site D (wet, dominated by *Molinia caerulea*), and none dying at site C (Table 3.6).

Table 3.5. Total proportion of marked individuals/tillers dying before the end of the experimental period.

	Total proportion dead
Grassland Species	
Agrostis capillaris	0.08
Anthoxanthum odoratum	0.05
Carex binervis	0
Carex panicea	0.03
Festuca ovina	0
Galium saxatile	0.15
Nardus stricta	0
Potentilla erecta	0.31
Vaccinium myrtillus	0
Mire Species	
Calluna vulgaris	0.18
Erica tetralix	0.13
Eriophorum angustifolium	0.03
Eriophorum vaginatum	0.02
Molinia caerulea	0
Narthecium ossifragum	0.02
Trichophorum cespitosum	0

Table 3.6. Proportion of individuals that died before the end of the experiment, by site, species and treatment. Blanks indicate species was not measured.

		Treatment and cut number						
		July 00 & 01		Oct 00	Mar 01	May & July 01		Control
	Site	1	2	1	1	1	2	
Grassland Species								
Agrostis capillaris	A	0.25	0	0	0.33	0	0	0
Agrostis capillaris	B	0.20	0	0	0	0	0	0.20
Anthoxanthum odoratum	A	0	0	0	1.00	0	0	0
Anthoxanthum odoratum	B	0	0	0	0	0	0	
Carex binervis	A			0		0	0	
Carex binervis	B	0	0	0	0	0	0	0
Carex panicea	A	0	0	0	0	0	0	0.17
Carex panicea	B	0	0					0
Festuca ovina	A	0	0	0	0	0	0	0
Festuca ovina	B	0	0	0	0	0	0	0
Galium saxatile	A	0	0	0	0.33	0.50	1.00	0
Galium saxatile	B	0	0	0.50	0.50	0	0	
Nardus stricta	A	0	0	0	0	0	0	0
Nardus stricta	B	0	0	0	0	0	0	0
Potentilla erecta	A	0.20	0	0			0	1.00
Potentilla erecta	B	0.17		0.50	0	0	0.50	
Vaccinium myrtillus	A	0	0		0	0	0	0
Vaccinium myrtillus	B	0	0	0	0	0	0	0
Average Prop Dead		0.05	0	0.06	0.14	0.03	0.09	0.10
Mire Species								
Calluna vulgaris	C	0	0	0	0	0	0	0
Calluna vulgaris	D	0.33	0	0.60	0.25	0.50	0	0.67
Erica tetralix	C	0	0.25	0	0	0	0.67	0
Erica tetralix	D	0.20	0	0.20	0	0	0.50	0
Eriophorum angustifolium	C	0	0	0	0	0	0	0
Eriophorum angustifolium	D	0.17	0	0	0	0	0	0.20
Eriophorum vaginatum	C	0	0	0.17	0	0	0	0
Eriophorum vaginatum	D	0	0	0	0	0	0	0
Molinia caerulea	C	0	0	0	0	0	0	0
Molinia caerulea	D	0	0	0	0	0	0	0
Narthecium ossifragum	C	0	0.20	0	0	0	0	0
Narthecium ossifragum	D	0	0	0	0	0	0	0
Trichophorum cespitosum	C	0	0	0	0	0	0	0
Vaccinium myrtillus	D	0	0	0	0	0	0	0
Average Prop Dead		0.05	0.03	0.07	0.02	0.04	0.08	0.06

3.4.2 Time taken to grow 5 cm: proportion of individuals achieving 5 cm

The proportion of individuals that achieved 5 cm growth during the experimental period varied with treatment and species (Table 3.7). For example, all *Nardus* *stricta* individuals in the March cut achieved 5 cm, but only three of the control *Festuca ovina* tillers did so (Fig 3.2; Fig 3.3). There were several cases of dwarf shrubs and forbs where none of the individuals grew by 5 cm. It should be noted that plants in treatments involving a cut in July 2001 had less time for re-growth than those in other treatments and so it would be expected that fewer individuals might achieve 5 cm growth.

Table 3.7. Proportion of individuals that achieved 5 cm growth during the experimental period.

	Treatment and Cutting Number						
	July 00 & 01		Oct 00	March 01	May & July 01		Control
	1	2	1	1	1	2	
Grassland Species							
Agrostis capillaris	0.33	0.50	0.88	0.67	0.75	0.50	1.00
Anthoxanthum odoratum	1.00	0.33	0.67	0.75	0.50	0.50	1.00
Carex binervis	0.50	0.67	0.83	1.00	0.86	0.57	1.00
Carex panicea	0.57	0.33	0.80	1.00	1.00	0.80	0.50
Festuca ovina	0.25	0.27	0.56	0.91	0.67	0.11	0.33
Galium saxatile	0	0	0.25	0.14	0	0.17	0
Nardus stricta	0.83	0.91	1.00	1.00	1.00	1.00	0.88
Potentilla erecta	0.09	0	0	1.00	1.00	0	0
Vaccinium myrtillus	0	0	0.25	0.57	0.57	0	0
Average Prop	0.40	0.33	0.58	0.78	0.70	0.41	0.52
Mire Species							
Calluna vulgaris	0.14	0	0.10	0.11	0	0	0
Erica tetralix	0	0.14	0	0	0.14	0	0.22
Eriophorum angustifolium	1.00	0.80	1.00	1.00	1.00	0.83	0.78
Eriophorum vaginatum	0.87	1.00	0.91	1.00	0.90	0.89	0.57
Molinia caerulea	1.00	0.40	1.00	1.00	1.00	0.29	1.00
Narthecium ossifragum	0.55	0.36	0.64	0.88	1.00	0.38	1.00
Trichophorum cespitosum	1.00	0.18	1.00	1.00	1.00	0.40	1.00
Average Prop	0.65	0.92	0.66	0.71	0.72	0.40	0.65

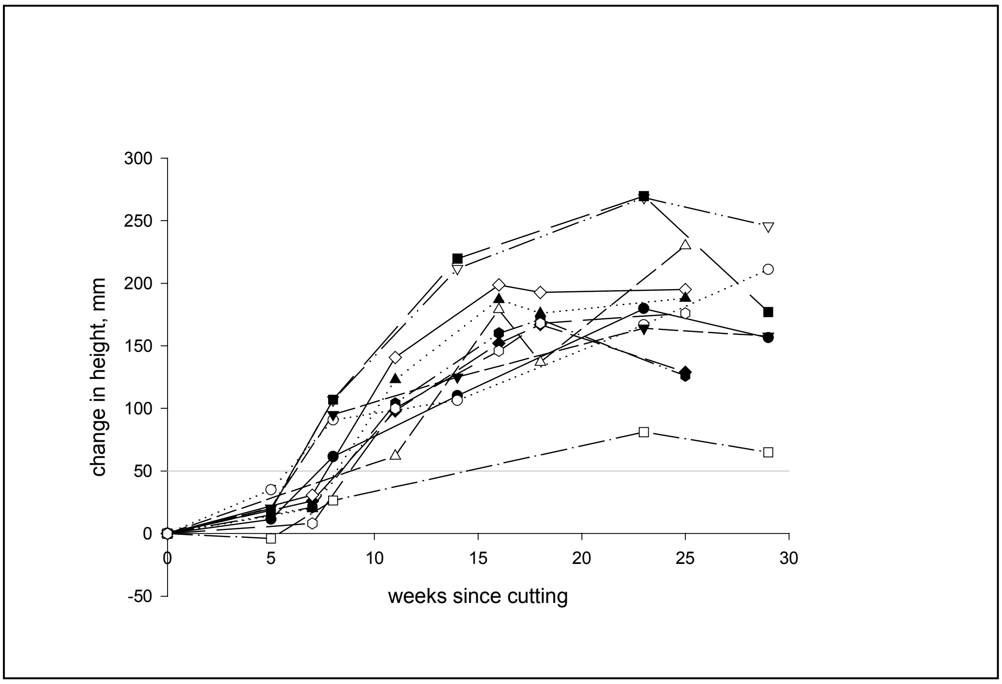

Fig 3.2. Growth of *Nardus stricta* tillers following cutting in March. All individuals achieve 5 cm growth, indicated by grey horizontal line.

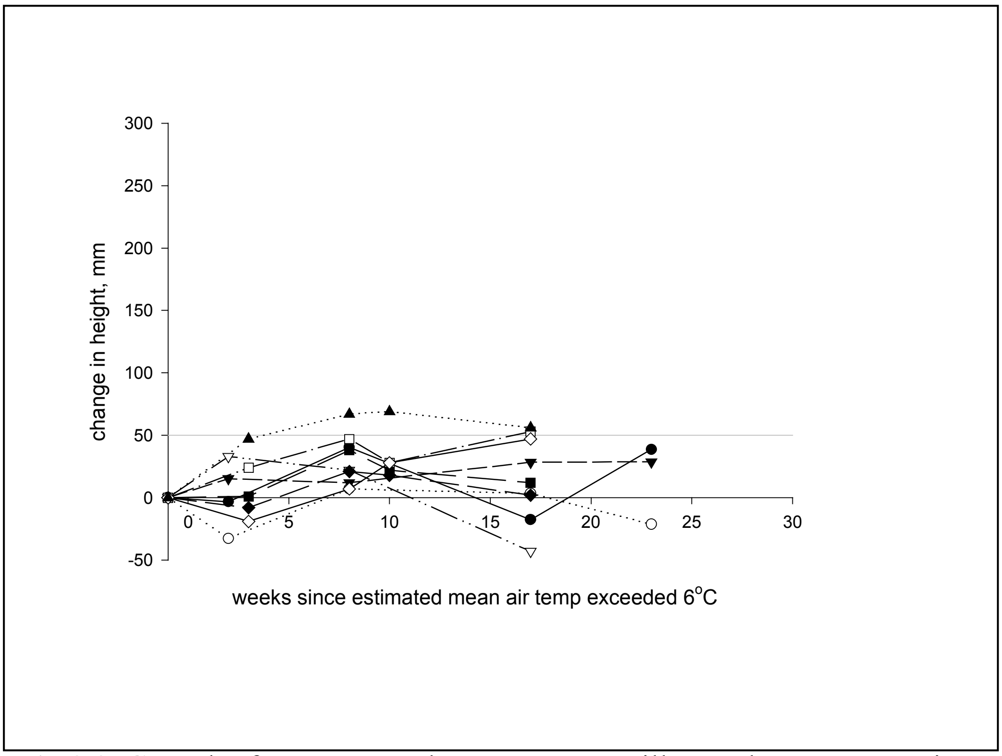

Fig 3.3. Growth of uncut control *Festuca ovina* tillers. Plants were cut in early May 2001. Most individuals do not achieve 5 cm growth (grey horizontal line).

3.4.3 Time taken to grow 5 cm: treatment level averages

Of the plants that did achieve 5 cm growth, the overall pattern of time taken to do so (Fig 3.4) varied between the seasonal treatments. As expected, plants in the October cut treatment took longest to grow to 5 cm, followed by the March cut treatments and then the other treatments. Average lengths of time taken by mire species to recover from clipping were slightly shorter than those of grassland species, except for the second cut of the May and July 2001 cut, where the opposite occurred, and the October cut, where recovery time was equal in both vegetation types. Generally, the length of time between cutting (or the start of the growing season for cuts carried out in the dormant period) was less for treatments cut at or before the start of the growing season compared to those cut later on in the growing season (Fig 3.4). As the longest live leaves on each plant were measured, comparison with control treatments should be made with great caution, as much older (and therefore more slow-growing) leaves were measured on uncut plants.

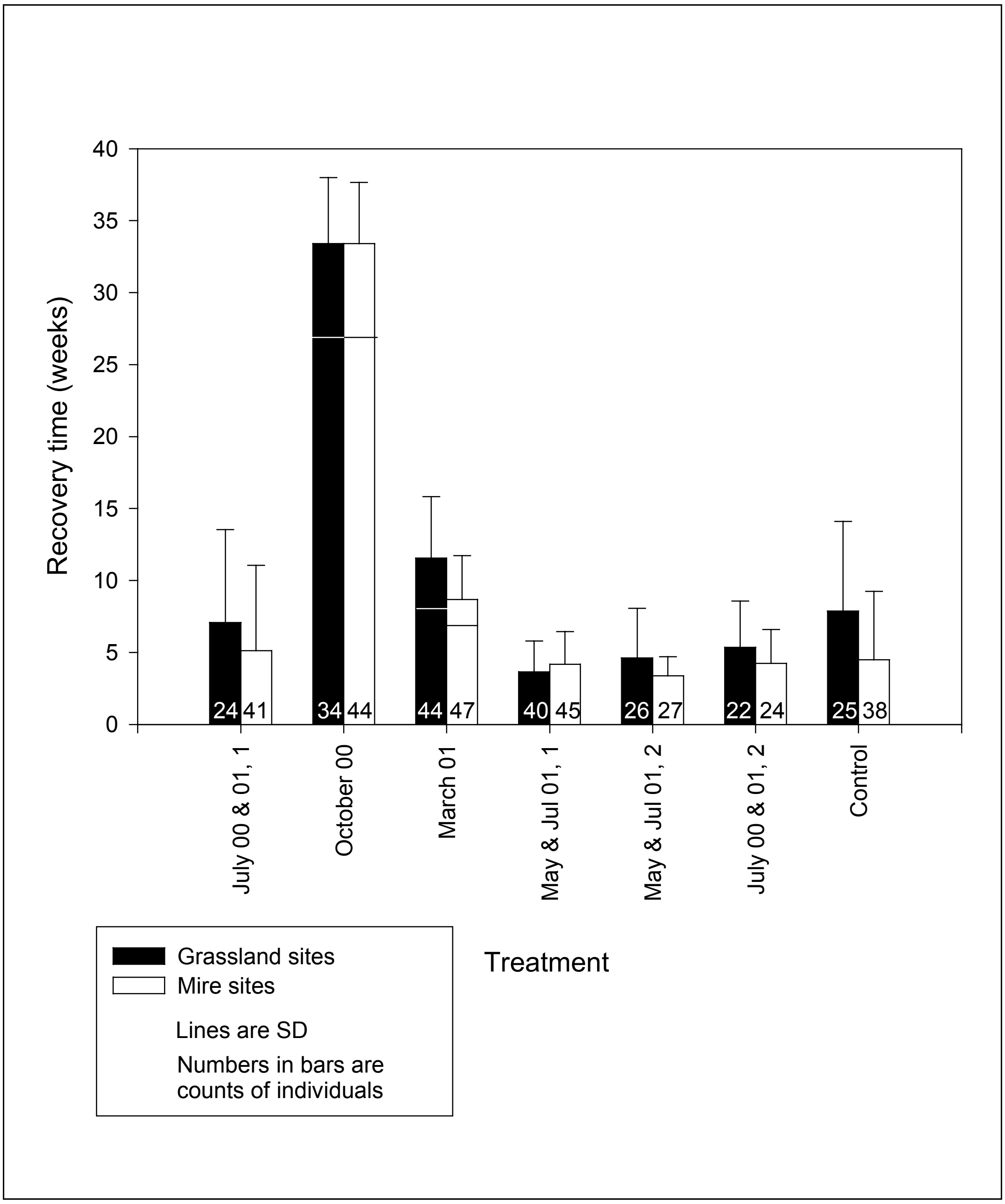

Fig 3.4. Average time taken for grassland and mire plants in cut treatments to grow 5 cm since cutting. Also for controls to grow 5 cm since estimated mean air temperature exceeded 6 °C. Individuals that did not grow by 5 cm were excluded from the calculation. Error bars are +1 S.D. The horizontal lines crossing the October and March treatments indicate the week when estimated mean air temperature exceeded 6 °C.

3.4.4 Time taken to grow 5 cm: seasonal variation between species

The average lengths of time taken to achieve 5 cm growth and the standard deviations (Table 3.8.b) cannot be used quantitatively since they include data for those plants that never grew 5 cm during the experimental period (assigned the arbitrary time of '54 weeks'). However, they can be used on the ordinal scale, by taking ranks.

<u>Grassland species</u>

The rank order of time to grow 5 cm was remarkably consistent between seasonal cuts for grassland species (Table 3.9). *Nardus stricta* was fastest during all seasons, with the sedge, *Carex panicea,* second fastest. The pasture grasses, *Agrostis capillaris* and *Festuca ovina*, were always ranked 3 or 4, and the forb, *Galium saxatile*, and the dwarf shrub, *Vaccinium myrtillus*, were consistently the slowest to achieve 5 cm growth.

<u>Mire species</u>

The rank order of time to grow 5 cm was much more dynamic between the mire species than between the grassland species. The dwarf shrubs, *Erica tetralix* and *Calluna vulgaris*, were consistently last to grow by 5 cm (Table 3.9). *Narthecium ossifragum* was usually ranked 5^{th} of 7, except in May when it was 4^{th}. The rankings of evergreen Cyperaceae family members, *Eriophorum vaginatum* and *Eriophorum angustifolium*, varied considerably through the year and did not always move in the same direction. *Eriophorum angustifolium* ranked 1^{st} in the July cut and October cut, but declined to 3^{rd} in the March cut. None of the non-wintergreen species were cut in the March treatment, as they had no live above-ground material. The non-wintergreen Cyperaceae member, *Trichophorum cespitosum*, ranked highly during spring cuts (its period of active growth) but less so at other times of the year. The deciduous grass, *Molinia caerulea*, was ranked 1^{st} in the March treatment, 2^{nd} in July, 3^{rd} in May and 4^{th} in October. Note: data for

July taken from first cut of July 2000 and 2001 treatment, data for May taken from first cut of May and July 2001 treatment.

Table 3.8. a) Average of time in weeks to grow 5 cm, including individuals that did not achieve 5 cm growth and that were assigned arbitrary value of 54 weeks; b) standard deviation of same data. Blanks are where sample size = 1. Sample sizes are given in Table 3.4.

Treatment	July 00 & 01		Oct 00	March 01	May & July 01		Control
a. Means	1	2	1	1	1	2	
Grassland Species							
Agrostis capillaris	40	30	39	26	17	31	4
Anthoxanthum odoratum	6	38	42	24	28	32	2
Carex binervis	28	23	34	9	10	26	26
Carex panicea	28	39	36	8	4	14	33
Festuca ovina	44	41	44	17	22	48	39
Galium saxatile	54	54	52	48	54	45	54
Nardus stricta	12	8	30	8	2	3	13
Potentilla erecta	50	54	54	21	7	54	54
Vaccinium myrtillus	54	54	50	31	25	54	54
Treatment mean	35	38	42	21	19	34	31
Mire Species							
Calluna vulgaris	47	54	53	50	54	54	54
Erica tetralix	54	47	54	54	47	54	45
Eriophorum angustifolium	2	15	32	8	3	11	19
Eriophorum vaginatum	13	4	32	10	9	9	26
Molinia caerulea	4	34	34	6	4	39	2
Narthecium ossifragum	27	36	45	16	7	36	4
Trichophorum cespitosum	7	45	33	7	3	34	1
Treatment mean	22	34	40	22	18	34	26
b. Standard deviations							
Grassland Species							
Agrostis capillaris	22	26	8	2	23	25	2
Anthoxanthum odoratum	0	28	11	20	30	26	
Carex binervis	36	27	10	2	19	26	
Carex panicea	25	24	10	0	1	22	23
Festuca ovina	19	22	9	12	24	17	22
Galium saxatile	0	0	4	15	0	22	
Nardus stricta	20	15	1	2	2	2	17
Potentilla erecta	15	0	0	6		0	0
Vaccinium myrtillus	0	0	8	22	27	0	0
Mire Species							
Calluna vulgaris	19	0	4	11	0	0	0
Erica tetralix	0	19	0	0	17	0	17
Eriophorum angustifolium	1	21	2	2	1	20	21
Eriophorum vaginatum	18	2	8	3	16	17	26
Molinia caerulea	2	27	1	2	1	25	1
Narthecium ossifragum	25	25	8	15	3	25	1
Trichophorum cespitosum	9	20	2	1	1	26	1

Table 3.9. Rank of species by average number of weeks to grow 5 cm in each of the four once-cut treatments. The species with the shortest time to grow 5 cm is ranked 1. Grassland species: Ns (*Nardus stricta*); Cp (*Carex panicea*); Ac (*Agrostis capillaris*); Fo (*Festuca ovina*); Gs (*Galium saxatile*); Vm (*Vaccinium myrtillus*). Mire species: Ea (*Eriophorum angustifolium*); Mc (*Molinia caerulea*); Tc (*Trichophorum cespitosum*); Ev (*Eriophorum vaginatum*); No (*Narthecium ossifragum*); Cv (*Calluna vulgaris*); Et (*Erica tetralix*). Gs and Vm were last equal in the July treatment.

	July	October	March	May
Grassland species	Ns 1	Ns 1	Ns 1	Ns 1
	Cp 2	Cp 2	Cp 2	Cp 2
	Ac 3	Ac 3	Fo 3	Ac 3
	Fo 4	Fo 4	Ac 4	Fo 4
	Gs 5	Vm 5	Vm 5	Vm 5
	Vm 5	Gs 6	Gs 6	Gs 6
Mire species	Ea 1	Ea 1	Mc 1	Tc 1
	Mc 2	Ev 2	Tc 2	Ea 2
	Tc 3	Tc 3	Ea 3	Mc 3
	Ev 4	Mc 4	Ev 4	No 4
	No 5	No 5	No 5	Ev 5
	Cv 6	Cv 6	Cv 6	Et 6
	Et 7	Et 7	Et 7	Cv 7

3.4.5 Time taken to grow 5 cm: effect of recovery time on species ranks

Grassland species

Again, grassland species rankings were less dynamic than those of mire species. The long-recovery treatment (July 2000 & 2001) resulted in the grass *Agrostis capillaris* overtaking the sedge, *Carex panicea*. The short-recovery treatment (May & July 2001) resulted in an improvement of the relative performance of *Galium saxatile*. *Nardus stricta* maintained its position of 1st ranked species, with swiftest regrowth, in both the long- and short-recovery treatments.

Table 3.10. Rank of species by average time taken to grow by 5 cm after the first and second of two cuts. Species with shortest time to grow 5 cm is ranked 1. Species abbreviations as in Table 3.9.

July 00 1	July 01 2	May 01 1	July 01 2
Ns 1	Ns 1	Ns 1	Ns 1
Cp 2	Ac 2	Cp 2	Cp 2
Ac 3	Cp 3	Ac 3	Ac 3
Fo 4	Fo 4	Fo 4	Gs 4
Gs 5	Gs 5	Vm 5	Fo 5
Vm 5	Vm 5	Gs 6	Vm 6
Ea 1	Ev 1	Tc 1	Ev 1
Mc 2	Ea 2	Ea 2	Ea 2
Tc 3	No 3	Mc 3	Tc 3
Ev 4	Mc 4	No 4	No 4
No 5	Tc 5	Ev 5	Mc 5
Cv 6	Et 6	Et 6	Cv 6
Et 7	Cv 7	Cv 7	Et 6

Mire species

Again, the dwarf shrubs were consistently last to achieve an average of 5 cm growth following cutting in both the long- and short- recovery treatments. The long-recovery treatment increased the relative performances of *Eriophorum vaginatum* and *Narthecium ossifragum*, while decreasing the relative performance of *Eriophorum angustifolium*, *Molinia caerulea* and *Trichophorum cespitosum*. The short-recovery treatment also increased the relative performance of *Eriophorum vaginatum*, while, again, *Trichophorum cespitosum* and *Molinia caerulea* decreased in relative performance.

Table 3.11. Rank order of time taken by individuals in control treatments to grow 5 cm in 2001. Measurements were made from the time estimated mean air temperature exceeded 6 ^{o}C.

	Uncut Controls	
Grassland Species	Ac	1
	Ns	2
	Cp	3
	Fo	4
	Gs	5
	Vm	5
Mire Species	Tc	1
	Mc	2
	No	3
	Ea	4
	Ev	5
	Et	6
	Cv	7

Grassland species control rankings

The uncut control grassland species showed a different pattern of relative time to grow 5 cm from the cut treatments. In the cut treatments, *Nardus stricta* was consistently first (Table 3.9), but in the controls, *Agrostis capillaris* was quickest (Table 3.11). Otherwise, the same pattern occurs as seen for the first cuts in May and July (Table 3.9).

Mire species control rankings

The uncut mire species showed a different pattern of rank time to achieve 5 cm to the cut treatments, with the non-wintergreen graminoids, *Trichophorum cespitosum*, *Molinia caerulea*, and *Narthecium ossifragum*, growing most quickly, with the evergreen graminoids next, and finally the dwarf shrubs last (Table 3.11).

3.5 DISCUSSION

The teleological view of plant responses to herbivory is that their aim is to restore and maintain homeostatic growth patterns where all resources are used in a balanced way for optimal growth (Chapman & Lemaire, 1993). Logically, the quicker a plant is able to do this, the better it will perform in grazed systems. The results show that upland species take a range of lengths of time to achieve 5 cm growth following cutting in different seasons, and following cutting with different recovery times. How are these differences related to life-form and phenology?

In the grassland community, the dwarf shrub *Vaccinium myrtillus* and forb *Galium saxatile* were consistently last to achieve 5 cm growth. This results from the comparatively slow growth of the dwarf shrub, and the small stature of the forb. They are also the only non-graminoid plants measured in the grassland community. Similarly, in the mire community, the two evergreen dwarf shrubs, *Calluna vulgaris* and *Erica tetralix*, are last to grow 5 cm. The dwarf shrubs were also last in the uncut treatments, so their comparatively slow growth rates can be held responsible for their poor performance when cut. The evergreen dwarf shrubs are only capable of active growth during late spring/early summer (Floate *et al.* 1979), so herbivory at any other time is likely to result in the loss of current meristematic material that will not be replaced until the following growing season.

Being non-wintergreen incurs a cost to plants, as not all of the resources in the dying leaves can be recovered and stored by the plant, and in infertile habitats many species are evergreen (Grime, 2001). The non-wintergreen species in the mire community performed better than the evergreens in the uncut controls and in the March cut (when the non-wintergreen species were still below-ground), but performed less well at other times. Could being non-wintergreen be a strategy for avoiding winter-herbivory and then growing faster than competitors to dominate communities during summer?

Nardus stricta is commonly regarded as a slow-growing species (Perkins, 1968). However, this work, and other clipping experiments (Nicholson *et al.* 1970) show that, at least in the short-term, *Nardus stricta* is capable of growing more quickly than neighbouring species following simulated herbivory. Utilisation of *Nardus stricta* at this site is comparatively high (Holland, 2001), probably due to the nature of the sward, which is a fine-grained mosaic, forcing sheep to eat some *Nardus* with most bites.

The upland pasture grasses, *Agrostis capillaris* and *Festuca ovina* were expected to perform well under simulated herbivory, since they are generally considered to have swift growth rates and rapid tissue turnover (Grime, 2001). However, they consistently trailed *Nardus stricta* in the cut treatments. A possible reason for this is that the cutting method removed more of the plant than a sheep would normally consume. Additionally, *Nardus* may have a greater storage capacity in its rhizomes than do *Agrostis capillaris* or *Festuca ovina*, allowing it to mobilise resources more quickly.

Woody and herbaceous species require the activation or formation of new buds on older stems following defoliation (Matthew *et al.* 2001) and take longer to restore a positive carbon balance following defoliation (Lemaire, 2001). The lower survivorship of these groups is therefore not surprising. However, as grasses have a highly flexible growth form and well protected meristems (Chapman & Lemaire, 1993) high survival was expected for *A. capillaris*. Many of the deaths in this species occurred in the uncut controls, suggesting that it competes poorly with tall vegetation, or that it has short-lived tillers with rapid turnover. *C. vulgaris* also showed surprisingly high death rates in the control treatment at site D. This may relate to the fact that this site is very marginal for *Calluna*, due to the high water table. The deciduous dwarf shrub, *V. myrtillus*, had 100% survivorship. This species is known to persist well under defoliation (Welch *et al.* 1994) as it has sufficient phenotypic plasticity to form new shoots rapidly (Tolvanen & Laine, 1997).

Morphological plasticity (Bradshaw, 1965) is the ability of plants to replace existing (or grazed) tissues with parts with different characteristics (Grime & Mackey, 2002). Examples are the ability of *Festuca ovina* to produce very short, dense tillers under heavy grazing and trampling (Grime *et al.* 1990), and *Vaccinium myrtillus* to grow into a short, heavily branched form under heavy grazing (Ritchie, 1956). The short-recovery time treatment might be expected to result in individuals expressing this plasticity, and is perhaps the cause of the decline in rank position of *Vaccinium myrtillus* and *Festuca ovina* in this treatment.

A further criticism of the cutting experiment was that it was carried out in an area that had been grazed moderately heavily for more than a century, and then was fenced against herbivores. Until it was exclosed, morphs with short stature would have been commonest in the population. After fencing, a season elapsed when there was no grazing, encouraging tall morphs to dominate the sward. The cutting experiment might therefore have had different results if carried out in temporarily erected cages within a generally grazed sward, where short stature morphs would have been dominant. The high death rate of *Calluna vulgaris* might relate to the fact that these plants were suppressed for decades, suddenly had the grazing pressure lifted and then were cut to 6 cm the following year. Very little herbivory in the quadrats occurred by deer, but some quadrats had to be abandoned due to vole damage.

Some plant species are known to recover from defoliation by using reserves from non-defoliated ramets (Williams & Briske, 1991). For many of the species studied, the majority of ramets are probably closely spaced, giving a high probability of most ramets being cut. However the ramets of *Eriophorum angustifolium* are spaced 1-2 m apart, giving a low probability of most ramets being cut. This may explain the swift regrowth of *Eriophorum angustifolium* in some seasons.

There has been lengthy debate in the literature about overcompensation and whether it benefits plants (e.g. Belsky, 1986; Ferraro & Oesterheld, 2002). Since the growth of mature leaves only were measured on control plants, a rigorous comparison between cut and uncut is not possible. The observed increase in growth following cutting (for example in *Nardus stricta*, which achieved 5 cm growth much more quickly when cut than uncut) therefore cannot be used as evidence of overcompensation.

A major constraint on this work is that it simulated grazing by cutting all plants in an area of the sward to the same height. In reality, herbivory is usually selective, removing a greater proportion of available biomass of certain species than of others. Mowing is likely to affect subsequent plant-plant interactions differently to selective grazing (Kleijn & Steinger, 2002; Moretto & Distel, 1999). Additionally, cutting with shears does not simulate trampling, dunging or urinating, all of which may affect the regrowth of plants following herbivory (Baldwin, 1990). Studies of actual herbivory at this scale are difficult to control, and changes occur in response to a suite of herbivore impacts. This study has effectively demonstrated the importance of seasonal herbivory in terms of the interaction between life form and season of biomass loss on the ability of species to re-grow.

3.6 CONCLUSIONS

The main conclusions are:

- Dwarf shrubs and forbs have lower growth rates than graminiods and are generally slower to recover from tissue loss.

- *Nardus stricta* had surprisingly swift growth rates given its overall longevity and tiller turnover.

- In the grassland sites, cutting in different seasons had very little effect on the relative times taken by species to achieve 5 cm growth. This may relate to the fact that almost all of the species are evergreen.

- In mire sites, there were changes in the rank times taken by species to achieve 5 cm growth following cutting in different seasons. The non-wintergreen species grew more quickly in spring than the evergreen species.

- The effect of different recovery times was minimal in the grassland sites. In the mire sites, repeated cutting had a similar effect regardless of the recovery time; the non-wintergreen graminoids performed less well, and *Eriophorum vaginatum* performed better, following the second cut.