Demographic drivers of biomass carbon recovery in degraded perennial tussock grassland, with and without domestic grazing

Robert J. Holdaway[1*], Alan B. Rose[2], Claire L. Newell[3] and Fiona E. Carswell[1]

[1]Landcare Research, PO Box 69040, Lincoln 7640, New Zealand
[2]Upland Research, 14 Chartres Lane, Arrowtown 9302, New Zealand
[3]Korowai Ecology, 6 Victoria Street, Springfield 7681, New Zealand
*Author for correspondence (Email: holdawayr@landcareresearch.co.nz)

Abstract: Many of New Zealand's natural and induced tussock grasslands are in a degraded low-biomass state due to a combination of fire, overgrazing and weed invasion. The capacity of degraded grasslands to recover biomass is uncertain because legacies of degradation can strongly influence the demographic processes controlling ecosystem recovery. We develop a conceptual framework for understanding biomass carbon (C) flux in degraded perennial grassland based on demographic processes of growth, mortality and recruitment. We apply this framework to 22 years of data from *Chionochloa*- and *Festuca*-dominated perennial tussock grassland in the South Island high country, sampling two grazed sites and two sites retired from domestic grazing. Total biomass C stocks were assessed at site level using 174 temporary plots measured in 1989 and 2011. Long-term demographics were monitored using 24 permanent plots in which 7213 individual tussocks were tagged and monitored every 1–5 years from 1989 to 2011. Although biomass C stocks were generally low (2159 ± 494 kg C ha^{-1}), there was a significant increase in total biomass C over the 22-year period at the north-facing retired site of 92 ± 47 kg C ha^{-1} year^{-1}. Increases in total biomass C were generally due to recruitment and growth of tall tussock (*Chionochloa* spp.) and/or woody shrubs. Biomass C stock in grazed sites, and the retired south-facing site, declined by up to 65 kg C ha^{-1} year^{-1} or remained constant. Declines were due to dieback of the dominant short tussock (*Festuca novae-zelandiae*) across all treatments, and a lack of recruitment of tall tussock and shrub species. Our results suggest that retirement from grazing was not sufficient to ensure total biomass C gains after 22 years, and highlight the roles of recruitment limitation, shrub establishment and management history in controlling ecosystem recovery.

Keywords: biomass allometry; *Chionochloa*; ecosystem services; *Festuca*; marginal farmland; recruitment; seed limitation

Introduction

Grassland ecosystems are one of the most widespread terrestrial ecosystems in the world, and are an important contributor to global biogeochemical cycles and terrestrial productivity (Scurlock & Hall 1998). However, many of the world's grassland ecosystems are becoming increasingly degraded (Akiyama & Kawamura 2007; Miehe et al. 2010). New Zealand's grassland ecosystems have expanded considerably in extent following human settlement about AD 1280 (Wilmshurst et al. 2008) due to a combination of Māori-lit fires and active forest clearance for agriculture and human settlement (McWethy et al. 2010; McGlone et al. 2014). Tussock grassland (dominated by *Chionochloa*, *Festuca* and *Poa* species) currently occupies over 700 000 ha of the eastern South Island between 700 and 1500 m above sea level (Newsome 1987). While the extent of tussock grassland has increased since human settlement, pressures such as herbivore introductions, overgrazing, agricultural burning, and weed invasion have resulted in significant degradation of many natural and induced grassland ecosystems (e.g. O'Connor 1982; Treskonova 1991; Rose et al. 1995; Rose & Frampton 2007). Degraded grasslands typically have sparse grass cover, low standing biomass, low productivity, and are more susceptible to further degradation through erosion and drought (Hofstede et al. 1995; Sparrow et al. 2003; Akiyama & Kawamura 2007).

The capacity of degraded grasslands to recover is uncertain because legacies of degradation can strongly influence the demographic processes (e.g. recruitment, growth, and mortality) controlling recovery (Rose & Platt 1992; Sparrow et al. 2003; Standish et al. 2009). Legacies include management history, loss of topsoil, depletion of natural seed sources, changes in dominant species pool, and physical changes to the environment. While many studies have looked at recovery of species composition in degraded ecosystems (Hobbs & Norton 1996; Rose et al. 2004), relatively few have investigated recovery of biogeochemical properties such as biomass carbon (C) sequestration, despite evidence to suggest that ecosystem properties might respond favourably to restoration even when composition does not recover (Palmer et al. 1997). Management of grasslands for C gain is an emerging opportunity (Conant 2010), and although the largest pool of C in grasslands is in the soil (Qiu et al. 2013; Soussana et al. 2004), New Zealand's tussock grassland species are perennial, long-lived, and can accumulate relatively high biomass. For example, Payton and Pearce (2009) reported total biomass C stocks of 18 Mg C ha^{-1} for *Chionochloa rigida* grassland, with over two-thirds of this total being root and litter biomass. These stocks are in the upper range of biomass C stocks reported for China's grasslands (1–24 Mg C ha^{-1}; Fan et al. 2008). Furthermore, ecosystem recovery via succession of induced grassland ecosystems back into woody-dominated shrubland or forest has the potential

to add a substantial additional pool of biomass C (Zavaleta & Kettley 2006; Walker et al. 2009).

Demographic processes of tree populations have been studied to better understand controls of net biomass change in forests (Botkin et al. 1972; Coomes et al. 2012) and these principles could also be applied to long-lived perennial tussock grasslands (Rose et al. 1995; Oliva et al. 2005). The demographic processes of recruitment, growth, and mortality vary with plant size structure, composition, time since disturbance, and with management (Coomes et al. 2012). Large areas of degraded grassland in New Zealand have recently become public conservation land through Nature Heritage Fund acquisitions and the tenure review process (e.g. the 68 000-ha Hakatere Conservation Park, Canterbury). It is thought that retirement from agricultural grazing, with the associated reduction in burning, has the potential to alter demographic processes and promote biomass recovery by reducing mortality, increasing growth and standing biomass of existing tussocks, and increasing plant recruitment (Rose et al. 1995; Su et al. 2003; Cipriotti & Aguiar 2012). Here, we develop a theoretical framework to address the question of whether grazing management affects the demographic drivers of biomass C change in degraded tussock grasslands. We apply this framework to 22 years of data from paired grazed and retired tussock grassland sites in New Zealand to test whether retirement from grazing promotes ecosystem recovery in the form of biomass C gain.

Materials and methods

Biomass C change in tussock grassland: a theoretical framework

To understand the demographic parameters driving biomass C sequestration in tussock grassland, we adapted a theoretical framework developed for above-ground C sequestration in forests (Coomes et al. 2012). This was possible because grasslands are governed by the same demographic processes (recruitment, growth, mortality) as forests, despite being ecologically very different systems. Here, we define biomass C as the sum of live above-ground, litter and root biomass pools. Biomass C of an individual tussock (C_i) can be predicted as an allometric function of its basal area (B_i) and height (H_i) (Guevara et al. 2002):

$$C_i = f(B_i, H_i) . \tag{1}$$

Total biomass C stock per unit area (C_{tot}) is

$$C_{tot} = \sum \frac{C_i}{plot\ area} . \tag{2}$$

Net biomass C sequestration ($SeqM$) between two time periods (t_0 and t_1) is therefore

$$SeqM = C_{tot,t1} - C_{tot,t0} . \tag{3}$$

Demographically, $SeqM$ is comprised of C gains due to growth of existing individuals ($ProdM$), C losses due to mortality and subsequent decomposition ($LossM$), and C gains due to recruitment and growth of new individuals ($RecrM$):

$$SeqM = ProdM - LossM + RecrM . \tag{4}$$

We present this framework using a 'carbon triangle' (Fig. 1a), a graphical model derived from Silvertown & Franco (1993). The
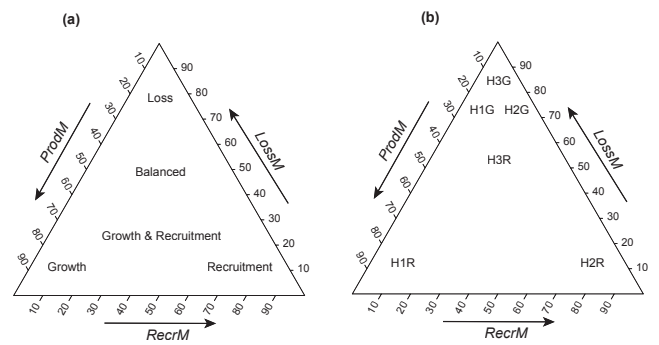
Figure 1. Carbon triangle framework illustrating the driving demographic processes and their hypothesised responses to grazing. Panel (a) gives the driving demographic processes and their location in triangle-space; panel (b) shows the hypothesised effects of retirement from grazing on demographic processes (alternative hypotheses H1–H3, G = grazed, R = retired; see theoretical framework section in main text for more details). Axes represent the relative contribution of each demographic carbon process to total net biomass carbon flux, and therefore sum to 100. *ProdM* = biomass carbon gain due to growth of existing individuals, *RecrM* = biomass carbon gain due to recruitment of new individuals into the population, *LossM* = biomass carbon loss due to mortality and reductions in size of existing individuals. A *LossM* of 50% or more indicates net biomass carbon loss.

three axes of the triangle represent the proportional contribution of the *ProdM*, *LossM*, and *RecrM* to total net biomass C flux. To avoid the complication of negative *ProdM* values caused by declines in biomass of live individuals, the *LossM* proportion includes both C lost due to mortality and biomass C lost due to dieback. This framework was used to visually assess the demographic processes driving net biomass C sequestration patterns (see Fig. 1a). Using the framework, we propose three (potentially competing) hypotheses for the effects of continued grazing (G) and retirement from domestic grazing (R) on the demographic drivers of biomass C stocks (Fig. 1b).

Hypothesis 1 (H1): Biomass C sequestration in the absence of grazing is driven by growth of existing individuals. Grazing (H1G) causes continued loss of biomass C through declines in biomass (low *ProdM*) and increased mortality (high *LossM*) whereas retirement from grazing (H1R) increases biomass C by increasing growth (high *ProdM*) and reducing mortality (low *LossM*) of tussocks. Recruitment of new individuals is unimportant.

Hypothesis 2 (H2): Biomass C sequestration in the absence of grazing is driven by recruitment of new individuals. Grazed sites (H2G) have low *RecrM* and continued loss of biomass C due to removal of above-ground biomass (low *ProdM*) and ongoing mortality (high *LossM*). Retirement from grazing (H2R) promotes biomass C sequestration due to recruitment of new tussocks and woody shrubs (high *RecrM*). The low density of existing individuals means that *ProdM* is unimportant.

Hypothesis 3 (H3): Biomass C sequestration is driven by ongoing mortality at both grazed and retired sites. Biomass loss due to mortality (*LossM*) is greater and *ProdM* and *RecrM* are lower in grazed sites (H3G) than retired sites (H3R), resulting in substantial biomass C loss at grazed sites. Any increases in

growth (*ProdM*) and recruitment (*RecrM*) at retired sites are offset by ongoing mortality (*LossM*).

Study area

The study took place in the Harper–Avoca catchments in New Zealand's South Island (43.10° S, 171.33° E). Vegetation[1] is primarily low-productivity tussock grassland dominated by a mixture of short-tussock (*Festuca novae-zelandiae* and *Poa cita*) and tall-tussock species (*Chionochloa macra* and *C. flavescens*). The area's management history is described in detail by Packard (1947) and Rose et al. (1995). Briefly, the natural forest cover of monospecific mountain beech (*Nothofagus solandri* var. *cliffortioides*) was burnt between 1860 and 1910 by European settler farmers, causing expansion of the adjacent natural tussock-dominated grasslands. These grasslands were grazed by sheep and cattle, and were burnt frequently up until c. 1950 (Rose & Platt 1992). Domestic grazing was removed from parts of the study area in 1955 and 1968. Wild deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), and hares (*Lepus europaeus*) have been present for about 100 years at variable densities depending on hunting pressure (Forsyth et al. 2010). Within this study area, four sites with different management histories were sampled: (1) south-facing grassland grazed by domestic and wild animals, (2) south-facing grassland retired from grazing by domestic stock in 1955, (3) north-facing grassland grazed by domestic and wild animals, and (4) north-facing grassland retired from grazing by domestic stock in 1968.

Temporary plots

Species composition, cover and tussock population structure were recorded on four transects established in 1989 at each site (*N* = 16 transects in total), using stratified random sampling that focused on the degraded tussock community. Transects were chosen to avoid occasional remnant patches of woody-dominated vegetation (Rose et al. 1990, 1995). Each transect had a marked origin and followed a fixed compass bearing from the valley floor at c. 700 to 1350 m a.s.l. A total of 174 unmarked 4-m^2 plots were established at intervals of 100 m along each transect, with a total of 40–48 plots per site. Transect origins and plot locations were permanently marked on aerial photos.

For each plot, all individuals of each tussock species rooted in the plot were measured. Basal diameter and maximum extended height of live tillers (pulled height) were recorded. For all shrubs, two orthogonal crown widths and natural (non-extended) height were measured. Estimated foliar cover of all vascular species having ≥5% cover was recorded in four cover classes (5–25%, 25–50%, 50–75%, 75–100%) and five height classes (<0.1 m, 0.1 – 0.3 m, 0.3–1 m, 1–2 m, 2–5 m). For the 2011 remeasurement, transect origins were re-located using photos and descriptions from 1989, the original compass bearings were followed, and plots were measured using the same methodology. These temporary plots provide the representative sample necessary to calculate site-level changes in biomass C stocks.

Permanent demography plots

In 1989, 22 stands that were representative of the tussock grassland in the area were selected from the four sites to monitor tussock demography under different grazing regimes (Rose & Platt 1992; Rose et al. 1990). Plots were subjectively located to sample at least 30 individual tussocks, and therefore varied in size from 4 to 80 m^2 depending on tussock density. Measurement methods were the same as for the unmarked plots (tussock basal diameter and pulled height, shrub crown width and natural height, foliar cover). All tussocks and shrubs were permanently tagged and mapped.

To assess the effects of wild animal grazing (predominantly hares), an additional fenced site and a paired control site were established in 1989. These were both located within the north-facing site that was retired from domestic grazing in 1968. Within each of these two sites, the same methods and measurement intervals were used to assess *Festuca* and *Poa* populations in five 10-m^2 plots. Trends in *Chionochloa* and shrub populations were also assessed using a single (non-replicated) 900-m^2 plot.

All permanent demography plots were remeasured at intervals of 1–5 years. All deaths were recorded and all new recruits were tagged and mapped. We analysed changes over time in total biomass C (calculation explained below), using measurements from 1989, 1991, 1996, 2001, 2006 and 2011, and calculated relative contributions of mortality (*LossM*), growth (*ProdM*) and recruitment (*RecrM*) using data from 1989 and 2011. With a total of 7213 tagged tussocks, these plots provide demographic data on growth, mortality and recruitment over 22 years.

Biomass C calculations

Tussock C was estimated for *Chionochloa flavescens* (eqn 5) and *C. macra* (eqn 6) using species-specific allometric relationships between total tussock C (C_{tus}) and basal cylindrical volume (V) (Johnson et al. 1988; Carswell et al. unpubl. report 2010; Fig. 2):

$$C_{tus} = 3.715 V^{0.795} \qquad r^2 = 0.94 \tag{5}$$

$$C_{tus} = 4.314 V^{0.800} \qquad r^2 = 0.90. \tag{6}$$

Total tussock C includes live tiller, root, dead tiller, and litter pools (Carswell et al. unpubl. report 2010). Basal cylindrical volume (V) was calculated from basal diameter (D) and pulled height (H) using the formula:

$$V = \frac{\pi D^2 H}{4} . \tag{7}$$

No species-specific allometric relationships were available for *Festuca novaezelandiae* or *Poa cita*; these species are most similar in growth form to *Chionochloa macra*, and so eqn (6) was used to estimate their C content.

Shrub volume and C density (kg C m^{-3}) were used to estimate total above-ground shrub C. Shrub volume (V_{shrub}) was calculated from measurements of orthogonal crown width (W_1 and W_2) and natural height (H_{shrub}):

$$V_{shrub} = W_1 W_2 H_{shrub}. \tag{8}$$

Shrub volume was converted into C using a shrub C density value of 1.029 kg C m^{-3} (Beets et al. 2009). For years where measurements of shrub orthogonal dimensions were missing, V_{shrub} was estimated from species-specific relationships between height and volume using 2011 data (Fig. 3). Shrub root C was estimated as 25% above-ground C (Cairns et al. 1997), and this value was added to shrub above-ground C to generate total shrub C.

---

[1] Plant names follow Nga Tipu o Aotearoa – New Zealand plants online database: http//nzflora.landcareresearch.co.nz (accessed July 2013).
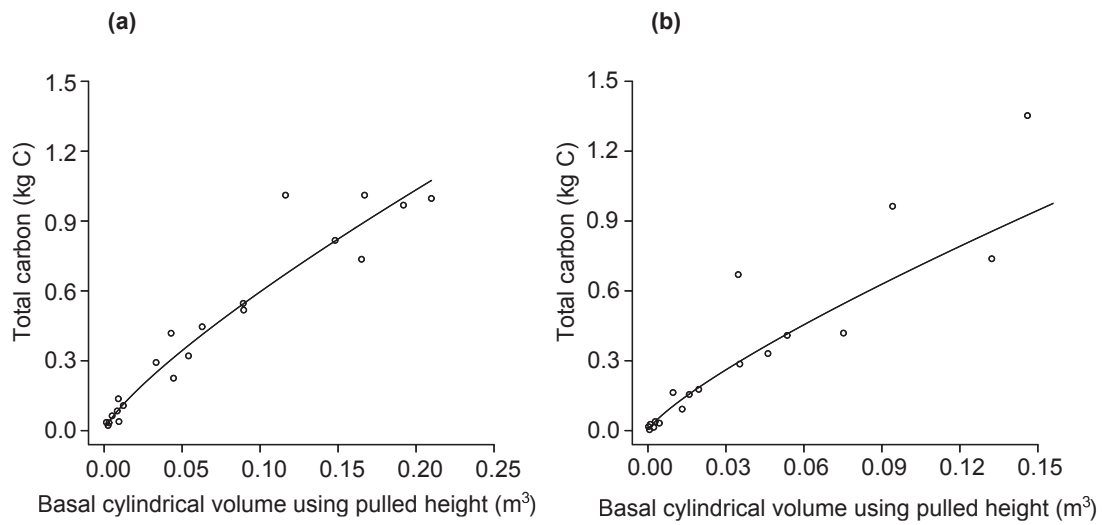
Figure 2. Allometric relationship between total carbon content and basal cylindrical volume calculated using pulled height for (a) *Chinochloa flavescens* and (b) *C. macra.* Total carbon content includes live tillers, roots, and litter. Fitted relationships: *C. flavescences* total carbon = 3.715(volume)$^{0.795}$ (r^2 = 0.94, P < 0.001), *C. macra* = 4.314(volume)$^{0.800}$ (r^2 = 0.90, P < 0.001).
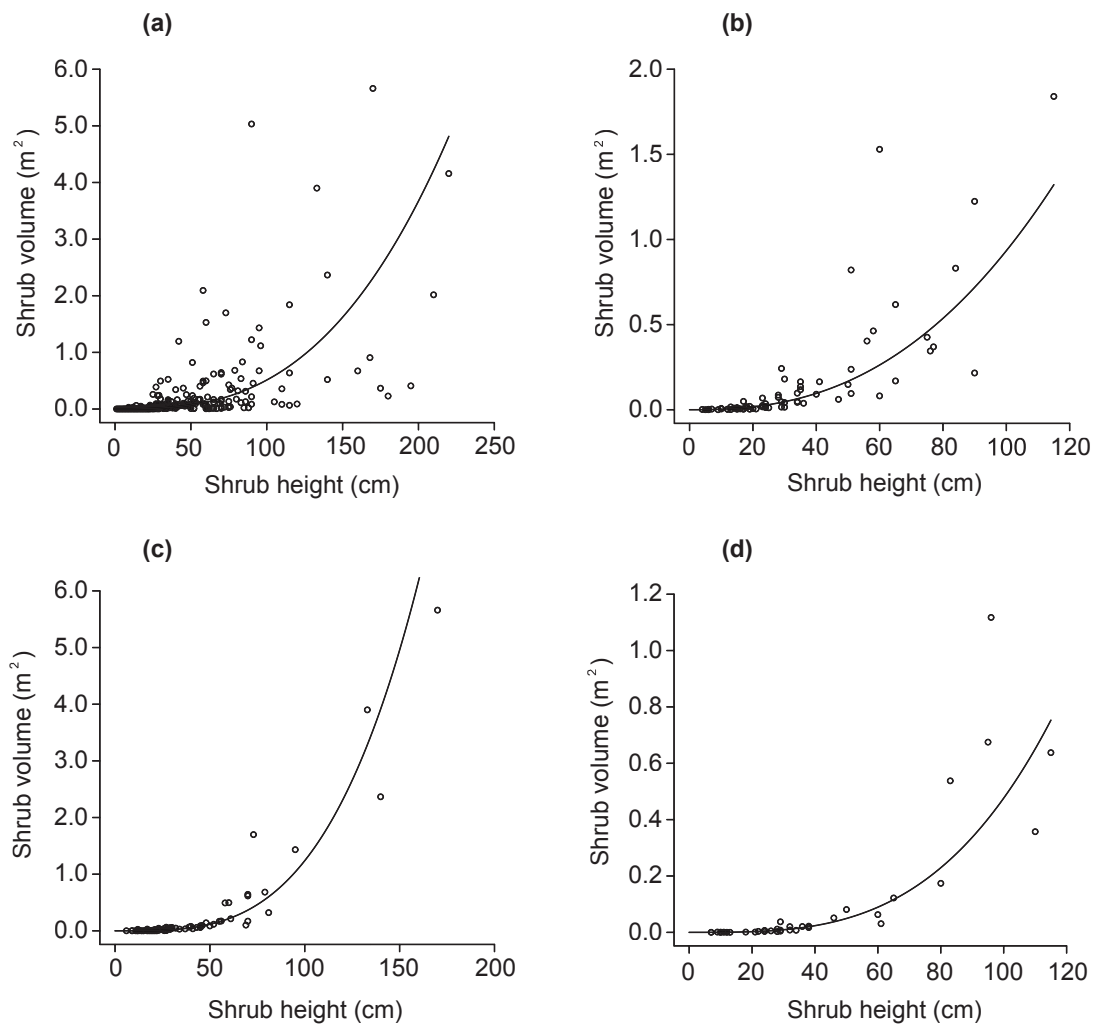
Figure 3. Shrub volume (m^3) as a function of shrub height (cm). Relationships shown for (a) all species, (b) *Discaria toumatou*, (c) *Corokia cotoneaster*, and (d) *Rosa rubignosa*. Fitted relationships: All species volume = 1.055 × 10^{-6}(height)$^{2.843}$ (r^2 = 0.75, P < 0.001); *Discaria toumatou* volume = 1.010 × 10^{-5} (height)$^{2.438}$ (r^2 = 0.84, P < 0.001); *Corokia cotoneaster* volume = 1.786 × 10^{-7}(height)$^{3.420}$ (r^2 = 0.74, P < 0.001); *Rosa rubignosa* volume = 1.339 × 10^{-7}(height)$^{3.276}$ (r^2 = 0.93, P < 0.001).

The biomass C associated with other live herbaceous species (e.g. non-tussock-forming grasses such as *Agrostis capillaris* and herbs such as *Celmisia spectabilis* (Asteraceae)) was assessed for two sites by destructively sampling a 6.5-cm-diameter circular sub-plot located at the centre of every second 4-m^2 temporary plot (i.e. 20 samples from each of two sites; grazed south-facing and retired south-facing). Samples were oven-dried at 60°C and weighed. A ratio of 0.47 was used to convert herbaceous biomass into C (IPCC 2006). Total C stocks in this pool ranged from 93 to 340 kg ha^{-1}, and averaged 230 (±26) kg ha^{-1} for the retired south-facing site and 232 (±43) kg ha^{-1} for the grazed south-facing site. These pools did not vary significantly between sites and previous years' data were not available. We therefore assumed this component did not change significantly between 1989 and 2011 and excluded the herbaceous (non-tussock) biomass C pool from all further analysis. Total biomass C stocks therefore represented the sum of total tussock C and total shrub C.

Statistical analysis

For the temporary plots the effects of site, treatment, and year on tussock density (number of tussocks per square metre), cover (% based on the geometric mean of cover-class data), tussock size (basal diameter), biomass C stock, and biomass C sequestration rate were analysed independently using ANOVA and Tukey HSD post hoc tests. Biomass C sequestration rates were calculated for each site, using transects as replicates ($N = 4$ transects per site) since transects were paired through time but plots were not. All other variables were analysed at the plot level ($N = 174$), except for tussock size, which was based on all individual plants at a particular site.

For the permanent demography plots we analysed trends in total biomass C over time, using linear mixed-effects models, with grazing treatment and year as fixed effects, and plot as a random effect on the Y-intercept to avoid temporal pseudo-replication. The effects of domestic grazing were analysed separately from the effects of excluding all grazing mammals at the fenced exclosure and control sites. These analyses were carried out using the *lme* function in the R package *nlme*. We used the demography plot data for the period 1989–2011 to calculate *ProdM* (growth of existing individuals), *LossM* (mortality), *RecrM* (recruitment and growth of new individuals), and *SeqM* (net carbon sequestration), and tested for domestic grazing effects using ANOVA and Tukey HSD tests. The relative contributions of *ProdM*, *LossM* and *SeqM* to net C sequestration were visually presented within the carbon triangle framework, using the *triax.plot* function in the R package *plotrix*. All statistical analyses were done in R version 2.11 (R Development Core Team 2010).

Results

Temporary plots

Total biomass C across all temporary plots in 2011 averaged 2210 ± 314 kg ha^{-1} (mean ± SE) and was higher in the retired sites compared with the grazed sites (2589 ± 329 kg ha^{-1} vs 1465 ± 186 kg ha^{-1}; Fig. 4a, ANOVA, $F_{3,170} = 10.36$, $P < 0.001$). The retired north-facing site showed a net increase in C from 1989 to 2011, with an average sequestration rate of 91.9 ± 47.4 kg C ha^{-1} year^{-1} (Fig. 4b; ANOVA, $F_{3,12} = 3.98$, $P = 0.035$). The other sites had either no net change or a decline in biomass C over the period (Fig. 4b).

Foliar cover of both tall (*Chionochloa* spp.) and short tussock (*Festuca novaezelandiae* and *Poa cita*) was low in the temporary plots, ranging from 0 to 10.1% for tall tussock and 2.2% to 12.3% for short tussock across all sites (Table 1). Tall-tussock cover was higher at the retired than the grazed sites in both 1989 (ANOVA, $F_{3,170} = 4.61$, $P = 0.003$) and 2011 ($F_{3,170} = 10.01$, $P < 0.001$). Shrub cover was also low, ranging from 0 to 17.6% across all sites. These results indicate that tussocks and shrubs comprised a relatively small fraction of total cover at all the sites, with the remaining cover (up to 95% in some sites) consisting of a mix of bare ground and invasive low-biomass herbs and grasses such as *Pilosella officinarum* (Asteraceae) and *Agrostis capillaris*.
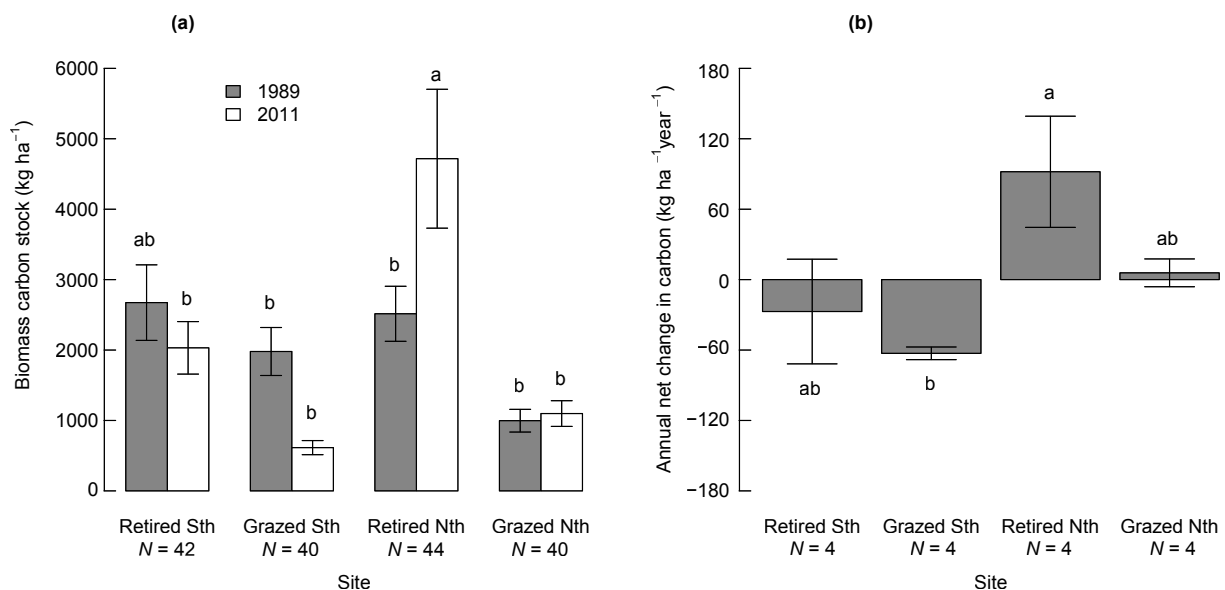
Figure 4. Effects of grazing and aspect on total biomass carbon stock and annual sequestration rate over a 22-year period. Both total biomass carbon stock (a) and annual sequestration rate (b) are based on the temporary-plot data. Sites differ in their grazing regime (grazed or retired), and their aspect (south and north facing). Error bars are ±SE with N = number of plots per site for (a) and number of transects per site for (b). Total biomass carbon stock includes all live above-ground, root, and litter biomass. Nth = north facing, Sth = south facing.

Table 1. Biomass carbon, size, density and cover by vegetation type for the 174 temporary plots. Standard errors are in brackets. *SeqM* = net annual biomass carbon sequestration rate, calculated at transect level ($N=4$). Biomass carbon, plant density, and percentage cover are all calculated with plot as the level of replication. Average plant size is represented by mean diameter (cm, for tall tussock and short tussock) or by height (m, for shrub category). Significant differences 1989–2011 are expressed as: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Site	Plant group	SeqM (kg C m⁻² year⁻¹)	Biomass carbon (kg C ha⁻¹)			Diameter (cm) or height (m)			Density (plants m⁻²)			Cover (%)		
			1989	2011	Sig.	1989	2011	Sig.	1989	2011	Sig.	1989	2011	Sig.
Retired north-facing	Tall tussock	−4 (5)	469 (178)	383 (121)		11.2 (2.1)	5.3 (1)	***	0.43 (0.22)	1.13 (0.42)		2.1 (0.9)	3.6 (1.2)	
	Short tussock	−46 (32)	1534 (258)	780 (111)	***	9.3 (1.1)	4.6 (0.7)	***	4.82 (0.63)	5.01 (1.13)		12.3 (1.3)	7.2 (0.8)	***
	Shrub	143 (38)	512 (238)	3554 (997)	***	0.36 (0.04)	0.37 (0.05)		0.53 (0.3)	1.54 (0.42)	**	4.3 (1.2)	17.6 (2.5)	***
Grazed north-facing	Tall tussock	0 (0)	0 (0)	0 (0)		0 (0)	0 (0)		0 (0)	0 (0)		0 (0)	0 (0)	
	Short tussock	−5 (6)	795 (135)	696 (126)		8 (1.04)	5.7 (0.98)	***	4.74 (1.06)	2.86 (0.67)	*	5.9 (1.3)	5.3 (0.9)	
	Shrub	10 (9)	202 (111)	402 (147)		0.33 (0.05)	0.33 (0.04)		0.15 (1.05)	0.32 (0.14)		1.3 (0.5)	1.8 (0.6)	
Retired south-facing	Tall tussock	20 (42)	939 (445)	1305 (381)		14.6 (2.7)	10 (1.9)	*	0.4 (0.11)	1.06 (0.32)	*	4.1 (1.5)	10.1 (2.7)	*
	Short tussock	−51 (20)	1724 (352)	623 (102)	**	6.3 (0.9)	2.9 (0.5)	**	5.27 (0.28)	8.31 (1.41)	*	5.6 (1.1)	5.4 (1.3)	
	Shrub	4 (3)	10 (5)	104 (51)		0.24 (0.01)	0.26 (0.03)		0.07 (0.02)	0.17 (0.1)		0 (0)	1.9 (1)	
Grazed south-facing	Tall tussock	−3 (3)	108 (99)	31 (19)		52.5 (6.1)	8.5 (1.3)	**	0.01 (0.01)	0.05 (0.02)	**	0.3 (0.3)	<0.1 (0)	
	Short tussock	−58 (6)	1717 (287)	467 (75)	***	4.7 (0.7)	3.3 (0.5)	***	5.16 (1.53)	5.63 (0.6)		2.2 (0.7)	5 (0.9)	
	Shrub	−2 (4)	155 (133)	116 (70)		0.53 (0.08)	0.39 (0.04)		0.04 (0.01)	0.07 (0.03)		0.3 (0.3)	0.8 (0.5)	*

Table 2. Summary carbon data and demographic indicators by vegetation type for the 22 permanent demography plots. *SeqM* = net annual biomass carbon sequestration rate, $N=7$ for the retired sites and $N=4$ for the grazed sites (excluding exclosure and control plots). Standard errors are given in brackets. Average size is represented by mean diameter (cm, for tall tussock and short tussock) or by height (m, for shrub category). Significance (Sig.) between years based on mixed-effects model using entire 1989–2011 dataset is indicated by *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Site	Plant group	SeqM (kg C m⁻² year⁻¹)	Biomass carbon (kg C ha⁻¹)			Diameter (cm) or height (m)			Density (plants m⁻²)		
			1989	2011	Sig.	1989	2011	Sig.	1989	2011	Sig.
Retired north-facing	Tall tussock	12 (11)	1454 (749)	1715 (722)		11.78 (1.11)	10.1 (0.73)		1.24 (0.65)	1.79 (0.84)	***
	Short tussock	−28 (15)	1614 (664)	989 (409)	***	6.61 (0.46)	6.26 (0.41)		6.61 (2.40)	5.39 (2.06)	*
	Shrub	34 (39)	286 (188)	1034 (796)		0.19 (0.02)	0.25 (0.04)	***	0.96 (0.61)	1.29 (0.44)	
Grazed north-facing	Tall tussock	0 (0)	0 (0)	0 (0)		0 (0)	0 (0)		0 (0)	0 (0)	
	Short tussock	−3 (22)	1501 (419)	1438 (527)		7.33 (0.44)	9.25 (0.73)	*	5.10 (1.86)	3.60 (1.33)	*
	Shrub	4 (4)	1.6 (1.3)	90 (89)	*	0.18 (0.66)	0.28 (0.19)		0.05 (0.03)	0.10 (0.04)	*
Retired south-facing	Tall tussock	87 (22)	2465 (1388)	4371 (1758)	***	5.62 (0.42)	4.73 (0.20)		2.76 (1.32)	7.73 (2.34)	***
	Short tussock	−2 (9)	736 (365)	688 (275)		5.97 (0.62)	4.60 (0.42)	*	2.81 (1.45)	4.36 (2.30)	**
	Shrub	7 (5)	0 (0)	163 (102)	**	0 (0)	0.23 (0.02)		0 (0)	1.23 (1.1)	*
Grazed south-facing	Tall tussock	−0.1 (0.1)	11 (11)	8.6 (8.6)		11.0 (NA)	12.0 (NA)		0.03 (0.03)	0.03 (0.03)	
	Short tussock	−8 (11)	777 (391)	604 (187)		3.92 (0.34)	3.80 (0.27)		5.38 (0.90)	5.23 (1.21)	
	Shrub	<0.1 (<0.1)	0 (0)	0.02 (0.02)		0 (0)	0.08 (NA)		0 (0)	0.01 (0.01)	

Short-tussock size declined by 29–54% and biomass by 12–73% across all sites over the 22 years, and these declines were statistically significant with the exception of the grazed north-facing site where the average size and density of tussocks declined by 29% and 40% (respectively) but declines in biomass C and percent cover were not significant (Table 1). These results indicate that widespread short-tussock fragmentation and mortality occurred over the 22-year period independently of grazing management. Where initially present, average tall-tussock diameter declined across sites, and there was a 165% increase in tall-tussock plant density at the retired south-facing site, indicating an increase in the number of small individuals in the population. Tall-tussock biomass C did not change significantly at any site over the 22 years (Table 1). There was a three-fold increase in shrub cover at the retired north-facing site, as well as a significant increase in shrub density, but no change in average shrub height (Table 1).

Permanent plots

The permanent demography plots had higher tussock plant density than the stratified-random temporary plots (Table 2 cf. Table 1) in both 1989 (0.84 ± 0.42 vs 0.20 ± 0.06 plants m^{-2}) and 2011 (2.03 ± 0.71 vs 0.55 ± 0.11 plants m^{-2}), resulting in higher tussock biomass C in the demography plots than in the temporary plots in 1989 (816 ± 352 vs 381 ± 122 kg C ha^{-1}) and 2011 (1278 ± 473 vs 428 ± 105 kg C ha^{-1}). However, average biomass C in the demography plots was similar to that in the temporary plots in both 1989 (2061 ± 350 vs 2046 ± 195 kg C ha^{-1}) and 2011 (2238 ± 531 vs 2210 ± 314 kg C ha^{-1}), likely reflecting lower shrub biomass C in demography plots compared with temporary plots (62 ± 41 vs 381 ± 122 kg C ha^{-1} in 1989 and 274 ± 170 vs 1134 ± 299 kg C ha^{-1} in 2011).

Permanent demography plots located in grazed sites had lower total biomass C compared with those in retired sites (Fig. 5; mixed-effects-model (MEM) grazing effect $t_{1,20} = -2.9$, $P = 0.007$), but did not change over time (MEM year effect $t_{1,108} = -0.46$, $P = 0.64$). However, total biomass C stock increased over time for retired sites (MEM year × grazing interaction, $t_{1,108} = 3.05$, $P = 0.003$), particularly the retired north-facing site (Fig. 5b). Individual biomass C pools from the permanent plots showed similar patterns to the temporary plots, with increases in tall tussock and shrub biomass, particularly at the retired sites, and significant declines in short-tussock biomass over time across some but not all sites (Table 2).

Declines in short-tussock biomass of 72% and 84% were recorded for the fenced exclosure and unfenced control sites respectively (Fig. 6a; MEM year effect $t_{1,48} = -5.93$, $P < 0.001$). There was no effect of grazing on changes in short-tussock biomass over time (MEM year × grazing interaction $t_{1,48} = 1.66$, $P = 0.10$). Although not replicated, increases in tall-tussock and shrub biomass were observed for both the fenced exclosure and control plots (Fig. 6b).
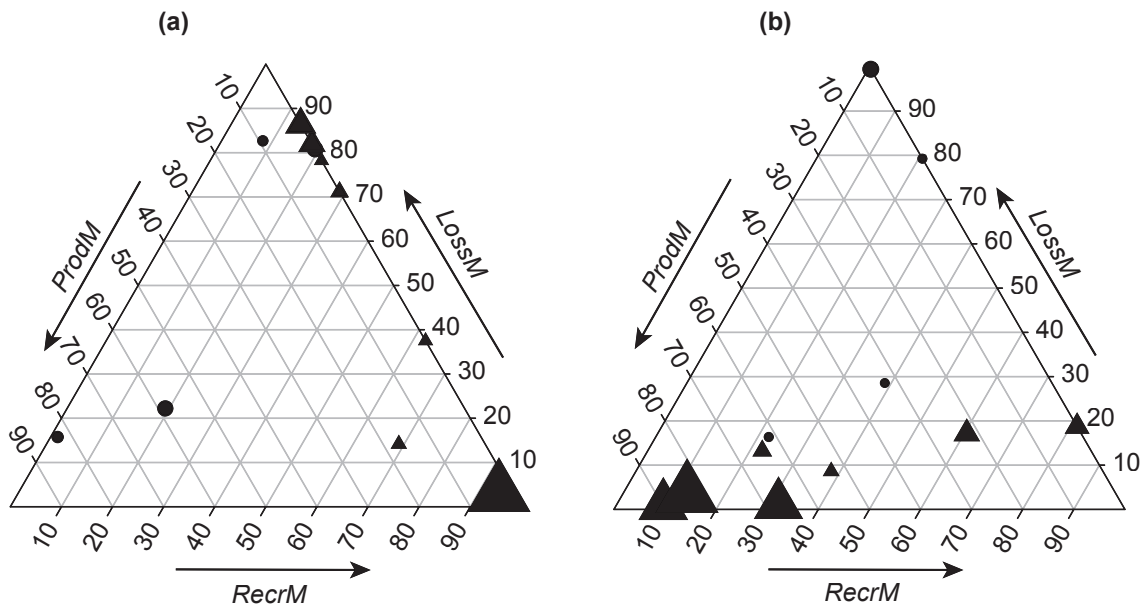
Demographic drivers

For the permanent demography plots, biomass growth of existing tussocks and shrubs (*ProdM*) varied among the four sites (ANOVA $F_{3,18} = 3.92$, $P = 0.02$) reflecting significantly higher *ProdM* on the retired south-facing site than the retired north-facing site (65.14 ± 23.94 vs 1.22 ± 1.22 kg C $ha^{-1}year^{-1}$; Tukey HSD $P = 0.03$) rather than grazing effects. Differences in *ProdM* among all other sites were non-significant. Biomass C loss due to mortality (*LossM*) averaged 25.48 ± 6.68 kg C $ha^{-1}year^{-1}$, and was similar among sites (ANOVA, $F_{3,18} = 2.91$, $P = 0.06$) and grazing treatments ($F_{1,20} = 0.11$, $P = 0.74$). Biomass C gain due to recruitment and growth of new individuals (*RecrM*) averaged 33.22 ± 12.18 kg C $ha^{-1}year^{-1}$ and was higher at retired sites compared with grazed sites (48.60 ± 18.02 vs 6.29 ± 2.48 kg C $ha^{-1}year^{-1}$); however, because of the high variability in *RecrM* among plots, this treatment effect was not significant (ANOVA, $F_{1,20} = 3.07$, $P = 0.09$). In summary, biomass C loss occurred at both grazed and retired north-facing sites, but C gains were primarily due to recruitment and subsequent growth of shrubs on retired sites (Table 2; Fig. 7a). In contrast, net sequestration occurred on south-facing sites due to a combination of the growth of existing tussocks (*ProdM*) and recruitment and growth of new individuals (*RecrM*) (Table 2; Fig. 7b).
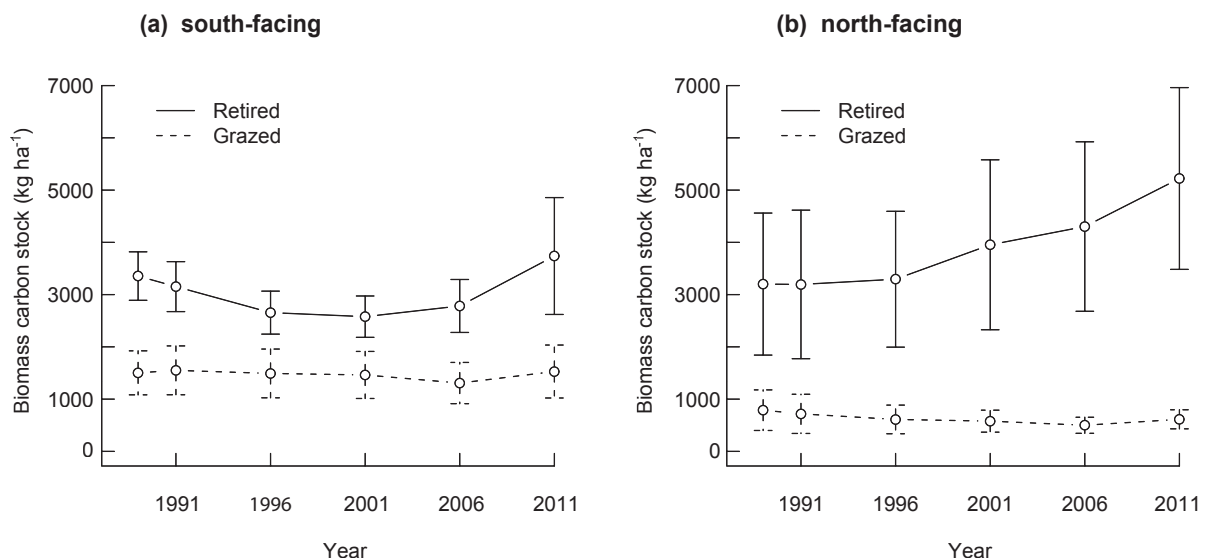
Figure 5. Variation in total biomass carbon stock in demography plots over a 22-year period. Data are from (a) south-facing and (b) north-facing grazed and retired sites. Error bars are ±SE.
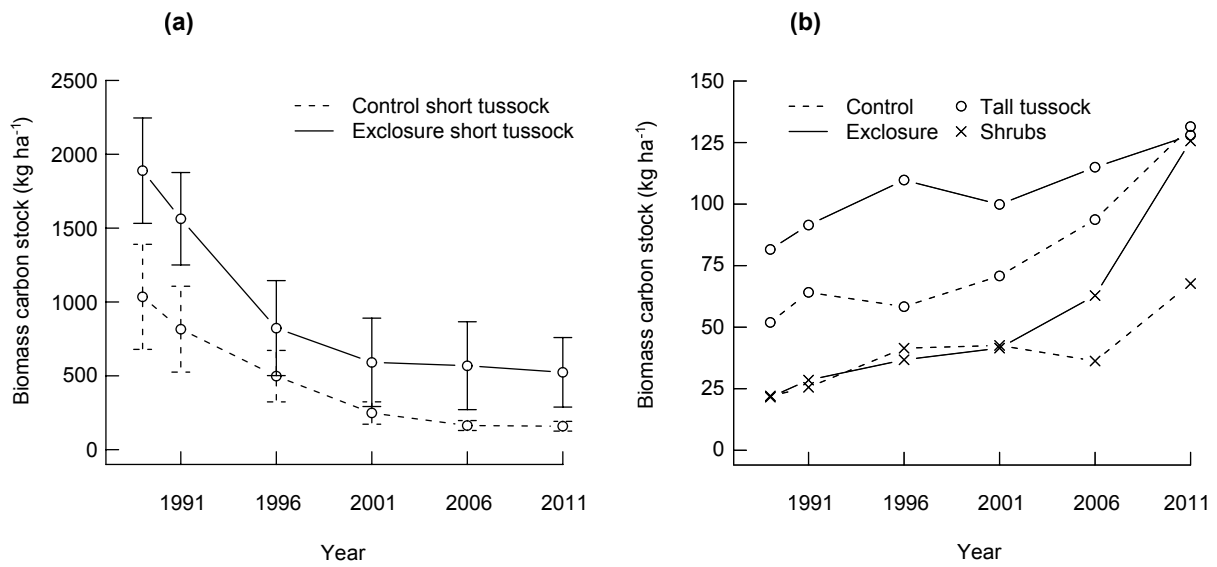
Figure 6. Biomass carbon stock changes over 22 years for control and fenced exclosure plots. Data are divided into (a) short-tussock biomass and (b) tall-tussock and shrub biomass. Control plots are retired from agricultural grazing but are grazed by hares (*Lepus europaeus*). Error bars are ±SE.

Figure 7. Demographic drivers of net biomass carbon (C) change for (a) north-facing sites and (b) south-facing sites based on data from permanent demography plots. Circles represent grazed sites, triangles retired sites. Symbol size scales proportionally to absolute net C change. Axes represent the relative contribution of each demographic carbon process to total net biomass C flux, and therefore sum to 100. *ProdM* = biomass C gain due to growth of existing individuals, *RecrM* = biomass C gain due to recruitment of new individuals into the population, *LossM* = biomass C loss due to mortality and reductions in size of existing individuals. A *LossM* of 50% or more indicates net biomass C loss.

Discussion

Effects of grazing on grassland C

We recorded only minor changes in C stocks over a 22-year period, with a maximum sequestration rate of 92 ± 47 kg C ha^{-1} year^{-1} for the retired north-facing site, and no change or losses of up to 65 kg C ha^{-1} year^{-1} for the other grazed and retired sites. Our demographic framework revealed mixed support for all three hypotheses (H1–H3), indicating that growth, recruitment and mortality all play important site-specific roles in determining the capacity of low-producing

perennial grassland ecosystems to sequester C. These small, variable and idiosyncratic long-term biomass C sequestration responses are similar to those observed for forests (Bardgett & Wardle 2003; Tanentzap et al. 2009; Holdaway et al. 2012) and suggest that retirement from grazing is not sufficient to ensure biomass C gains in New Zealand tussock grasslands at decadal timescales. An understanding of the effects of management activities on biomass C stocks in low-productivity grasslands is required to enable land managers to accurately assess the potential costs, benefits and trade-offs associated with agricultural grazing practices (Scurlock & Hall 1998;

Conant 2010; Dickie et al. 2011). Our results suggest that removal of agricultural grazing in these ecosystems may not lead to recovery of the pre-grazing state (Standish et al. 2009) and that a diverse range of management interventions may therefore be required to achieve significant biomass C gains.

Growth and capacity to recover

Growth (*ProdM)* is often viewed as the most important driver of biomass C sequestration, determined by initial density and intrinsic growth rates of individuals (Coomes et al. 2012). The low tussock density at our sites resulted in low *ProdM* values, and *ProdM* was only a significant determinant of net C flux at the south-facing retired site where tussock density was high. The low *ProdM* also suggests the intrinsic growth rates of tall-tussock grasses in New Zealand are relatively slow. Similarly, Lee et al. (2000) showed that heavy grazing of *Chionochloa pallens* had negative effects for up to 20 years and that full recovery of individual tussocks may take up to three decades. Annual C gain due to growth is also influenced by environmental factors, with the south-facing sites being typically cool and wet and the north-facing sites being dry and hot. Eddy covariance estimates of C gain for sparse tussock grassland in the Mackenzie Basin, New Zealand, showed large variability in net C sequestration between wet (gain of 410 kg ha^{-1}) and dry (loss of 90 kg ha^{-1}) years (Hunt et al. 2004). Our results support the view that tussock grass productivity is low and that growth is the main process driving biomass C change, but only when tussock density and cover are high.

Overcoming recruitment limitation

The low density of existing tall tussocks, particularly on grazed sites, could limit seed availability and recruitment. For example, Rose and Platt (1992) found that 93% of tall-tussock seedlings occurred within 70 cm of a mature adult tussock. Inter-tussock ground substrate may also influence seedling establishment. Rose and Platt (1992) also reported that seedling distribution varied greatly from high frequencies in native vascular and bryophyte mats to very low frequencies on exposed bare ground. In another study area, Tanentzap et al. (2009) found increase in size but no change in numbers of individuals for tussock grassland after 40 years of red deer control, and suggest that seed addition may be required to facilitate tussock regeneration. The limited recruitment ability of tall tussock (*Chionochloa* sp.) is further exacerbated by its strong mast-seeding behaviour (Kelly et al. 2000), and poor ability to colonise bare ground (Rose & Platt 1992; Lloyd et al. 2003). In tussock grasslands on the Patagonian steppe, seed distribution has been found to be more important than microsite availability for recruitment in tussock grassland (Aguiar & Sala 1997). These results suggest that seed limitation may be an important barrier to tall-tussock establishment.

For human-induced grasslands, cessation of grazing also can promote woody plant establishment (Cipriotti & Aguiar 2012), which may lead to biomass C gains. Recruitment of woody shrubs dominated net biomass C sequestration patterns at the north-facing retired site, while woody establishment at other sites was limited. This was most likely due to a combination of seed limitation and microclimate; with the retired north-facing site having higher local seed availability and a warmer microclimate (Mason et al. 2013a). Woody establishment into grassland can cause increases in biomass C, declines in soil C and complex responses by different components of above- and below-ground diversity (Dickie et al.

2011). However, woody establishment may also represent the natural trajectory of ecosystem recovery for induced grasslands such as those in our study area (Walker et al. 2009). Such trade-offs between biodiversity and ecosystem services are important to consider when assessing the likely trajectory of ecosystem recovery.

Short-tussock mortality

Mortality can exert a strong influence on net biomass C sequestration through individual plant death, and this effect is amplified when cohort-wide population senescence occurs (Kurz et al. 2008; Mason et al. 2013b). There is some evidence for cohort-type dynamics occurring in short tussock, with dieback and fragmentation of large individuals recorded throughout the four study sites, regardless of grazing treatment (Table 1). Rose and Frampton (2007) also recorded large and sudden declines in short-tussock cover in grazed and ungrazed grasslands. Reasons for such declines in short tussock are unclear. Historical large-scale burning could have led to the establishment of a relatively even aged cohort of short tussock (Rose et al. 1995), which may be undergoing natural senescence. Alternatively, Rose and Frampton (2007) attributed declines in short tussock to competition with the invasive herb *Pilosella officinarum* (formerly *Hieracium pilosella,* Asteraceae). Regardless of the cause, such mortality events can result in biomass C declines. In our study, losses from short-tussock mortality were somewhat buffered by recruitment of tall tussock and shrubs in retired sites, but not in grazed sites. This demonstrates the interactive effects that biological invasions, management legacies, and demographic processes have on the recovery of an ecosystem property such as biomass.

Limitations of non-destructive C estimation techniques

A limitation of this study is an inability to detect changes in above- vs below-ground biomass allocation. This is because the allometric models used to non-destructively estimate C stock assume that the ratio of above- to below-ground biomass is fixed. In contrast, grazing can alter the allocation of resources below ground, and the direction of the effect depends on site productivity and species' tolerance to grazing. For example, Frank et al. (2002) observed much greater stimulation of root productivity and shoots in naturally grazed grassland compared with exclosure plots in Yellowstone Reserve, USA. In contrast, McIntosh and Allen (1998) showed disproportional increases in root biomass inside exclosure plots in short-tussock grassland in New Zealand compared with plots grazed by sheep and rabbits. This supports the idea that New Zealand tussock grasslands may be intolerant of grazing by introduced mammals (Lee et al. 2000; Tanentzap et al. 2009), suggesting that grazing might reduce both above- and below-ground productivity in these systems. Further investigation of the effects of management on the ratio of above- to below-ground biomass in grasslands would be beneficial, especially if these data are incorporated into allometric biomass models.

Another limitation of our study is that we do not have any repeat-measured information on the soil C pool in our study area. Soil C is the largest C pool in grassland ecosystems, and it can show dynamic and variable responses to grazing management (Soussana et al. 2004; Derner & Schuman 2007; Qiu et al. 2013). However, there have been relatively few studies looking at the effect of domestic grazing on soil C in New Zealand tussock grasslands. McIntosh and Allen (1998) found no effect of grazing removal on soil C in short-tussock

grasslands after 16 years, despite a 43% increase in plant biomass. Basher and Lynn (1996) found conflicting effects of grazing removal on soil C after 45 years of grazing exclusion at two sites within 20 km of the current study area. Dickie et al. (2011) found that establishment of the invasive *Pinus nigra* into short-tussock grasslands resulted in a decline in soil C, but this was offset by a concurrent increase in above-ground woody biomass. Further research on the relationship between above-ground tussock biomass, woody plant invasion, root biomass and soil C is therefore required to properly understand the effects of ecosystem recovery and total C stocks.

Conclusions

Our study provides a framework for understanding the effects of grazing management on the demographic drivers of biomass C recovery. A demographic understanding informs management by identifying the key processes limiting biomass C gain, allowing management actions to be tailored to overcome these specific barriers. Our results highlight the role of recruitment limitation, shrub establishment and management history in controlling ecosystem recovery in degraded perennial tussock grasslands. Retirement from grazing was not sufficient to ensure biomass C gains. Land managers wishing to enhance biomass C in degraded human-induced perennial tussock grasslands may need to overcome multiple barriers to promote the establishment and growth of tall tussock, woody shrubs and ultimately forests.

References

Aguiar MR, Sala OE 1997. Seed distribution constrains the dynamics of the Patagonian steppe. Ecology 78: 93–100.

Akiyama T, Kawamura K 2007. Grassland degradation in China: Methods of monitoring, management and restoration. Grassland Science 53: 1–17.

Basher LR, Lynn IH 1996. Soil changes associated with cessation of sheep grazing in the Canterbury high country, New Zealand. New Zealand Journal of Ecology 20: 179–189.

Bardgett RD, Wardle DA 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84: 2258–2268.

Beets PN, Kimberley MO, Goulding CJ, Garrett LG, Oliver GR, Paul TSH 2009. Natural forest plot data analysis: carbon stock analysis and remeasurement strategy. Scion contract report available on request from the Ministry for the Environment, Wellington.

Botkin DB, Janak JF, Wallis JR 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60: 849–872.

Cairns MA, Brown S, Helmer EH, Baumgardner GA 1997. Root biomass allocation in the world's upland forests. Oecologia 111: 1–11.

Cipriotti PA, Aguiar MR 2012. Direct and indirect effects of grazing constrain shrub encroachment in semi-arid Patagonian steppes. Applied Vegetation Science 15: 35–47.

Conant RT (comp.) 2010. Challenges and opportunities for carbon sequestration in grassland systems: A technical report on grassland management and climate change mitigation. [FAO] Integrated Crop Management 9: 1–57.

Coomes DA, Holdaway RJ, Kobe RK, Lines ER, Allen RB 2012. A general integrative framework for modelling woody biomass production and carbon sequestration rates in forests. Journal of Ecology 100: 42–64.

Derner JD, Schuman GE 2007. Carbon sequestration and rangelands: A synthesis of land management and precipitation effects. Journal of Soil and Water Conservation 62: 77–85.

Dickie IA, Yeates GW, St. John MG, Stevenson BA, Scott JT, Rillig MC, Peltzer DA, Orwin KH, Kirschbaum MUF, Hunt JE, Burrows LE, Barbour MM, Aislabie J 2011. Ecosystem service and biodiversity trade-offs in two woody successions. Journal of Applied Ecology 48: 926–934.

Fan J, Zhong H, Harris W, Yu G, Wang S, Hu Z, Yue Y 2008. Carbon storage in the grasslands of China based on field measurements of above- and below-ground biomass. Climatic Change 86: 375–396.

Forsyth DM, Allen RB, Marburg AE, MacKenzie DI, Douglas MJW 2010. Population dynamics and resource use of red deer after release from harvesting in New Zealand. New Zealand Journal of Ecology 34: 277–287.

Frank DA, Kuns MM, Guido DR 2002. Consumer control of grassland plant production. Ecology 83: 602–606.

Guevara JC, Gonnet JM, Estevez OR 2002. Biomass estimation for native perennial grasses in the plain of Mendoza, Argentina. Journal of Arid Environments 50: 613–619.

Hobbs RJ, Norton DA 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4: 93–110.

Hofstede RGM, Castillo MXM, Osorio CMR 1995. Biomass of grazed, burned, and undisturbed Páramo grasslands, Colombia. I. Aboveground vegetation. Arctic and Alpine Research 27: 1–12.

Holdaway RJ, Burrows LE, Carswell FE, Marburg AE 2012. Potential for invasive mammalian herbivore control to result in measurable carbon gains. New Zealand Journal of Ecology 36: 252–264.

Hunt JE, Kelliher FM, McSeveny TM, Ross DJ, Whitehead D 2004. Long-term carbon exchange in a sparse, seasonally dry tussock grassland. Global Change Biology 10: 1785–1800.

IPCC 2006. 2006 IPCC guidelines for national greenhouse gas inventories. Vol. 4 Agriculture, forestry and other land use. Geneva, Switzerland, Intergovernmental Panel on Climate Change.

Johnson PS, Johnson CL, West NE 1988. Estimation of phytomass for ungrazed crested wheatgrass plants using allometric equations. Journal of Range Management 41: 421-425.

Kelly D, Harrison AL, Lee WG, Payton IJ, Wilson PR, Schauber EM 2000. Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). Oikos 90: 477–488.

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452: 987–990.

Lee WG, Fenner M, Loughnan A, Lloyd KM 2000. Long-term effects of defoliation: incomplete recovery of a New Zealand alpine tussock grass, *Chionochloa pallens*, after 20 years. Journal of Applied Ecology 37: 348–355.

Lloyd KM, Lee WG, Fenner M, Loughnan AE 2003. Vegetation change after artificial disturbance in an alpine *Chionochloa pallens* grassland in New Zealand. New Zealand Journal of Ecology 27: 31–36.

Mason NWH, Wiser SK, Richardson SJ, Thorsen MJ, Holdaway RJ, Dray S, Thomson FJ, Carswell FE 2013a. Functional traits reveal processes driving natural afforestation at large spatial scales. PloS ONE 8(9): e75219.

Mason NWH, Bellingham PJ, Carswell FE, Peltzer DA, Holdaway RJ, Allen RB 2013b. Wood decay resistance moderates the effects of tree mortality on carbon storage in the indigenous forests of New Zealand. Forest Ecology and Management 305: 177–188.

McGlone MS, Perry GLW, Houliston GJ, Connor HE 2014. Fire, grazing and the evolution of New Zealand grasses. New Zealand Journal of Ecology 38: 1–11.

McIntosh PD, Allen RB 1998. Effect of exclosure on soils, biomass, plant nutrients, and vegetation, on unfertilised steeplands, Upper Waitaki District, South Island, New Zealand. New Zealand Journal of Ecology 22: 209–217.

McWethy DB, Whitlock C, Wilmshurst JM, McGlone MS, Fromont M, Li X, Dieffenbacher-Krall A, Hobbs WO, Fritz SC, Cook ER 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. Proceedings of the National Academy of Sciences (USA) 107: 21343–21348.

Miehe S, Kluge J, von Wehrden H, Retzer V 2010. Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. Journal of Applied Ecology 47: 692–700.

Newsome PFJ 1987. The vegetative cover of New Zealand. Wellington, Water and Soil Directorate, Ministry of Works and Development. 153 p.

Oliva G, Collantes M, Humano G 2005. Demography of grazed tussock grass populations in Patagonia. Rangeland Ecology & Management 58: 466–473.

Packard WP 1947. Lake Coleridge catchment: A geographic survey of its problems. New Zealand Geographer 3: 19–40.

Palmer MA, Ambrose RF, Poff NL 1997. Ecological theory and community restoration ecology. Restoration Ecology 5: 291–300.

Payton IJ, Pearce HG 2009. Fire-induced changes to the vegetation of tall tussock (*Chionochloa rigida*) grassland ecosystems. Science for Conservation 290. Wellington, Department of Conservation. 42 p.

O'Connor KF 1982. The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. New Zealand Journal of Ecology 5: 97–107.

Qiu L, Wei X, Zhang X, Cheng J 2013. Ecosystem carbon and nitrogen accumulation after grazing exclusion in semiarid grassland. PloS ONE 8(1): e55433.

R Development Core Team 2010. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. ISBN 3-900051-07-0, http://www.R-project.org/.

Rose AB, Frampton CM 2007. Rapid short-tussock grassland decline with and without grazing, Marlborough, New Zealand. New Zealand Journal of Ecology 31: 232–244.

Rose AB, Platt KH 1992. Snow tussock (*Chionochloa*) population responses to removal of sheep and European hares, Canterbury, New Zealand. New Zealand Journal of Botany 30: 373–382.

Rose AB, Platt KH, Hall G 1990. Fescue tussock grassland on grazed and retired hillslopes, Harper-Avoca catchment, Canterbury. 1. Composition and tussock biomass. FRI Contract Report FW 90/14, prepared for the Department of Conservation (Investigation no. S7010/487). Rotorua, Forest Research Institute.

Rose AB, Platt KH, Frampton CM 1995. Vegetation change over 25 years in a New Zealand short-tussock grassland: Effects of sheep grazing and exotic invasions. New Zealand Journal of Ecology 19: 163–174.

Rose AB, Suisted PA, Frampton CM 2004. Recovery, invasion, and decline over 37 years in a Marlborough short-tussock grassland, New Zealand. New Zealand Journal of Botany 42: 77–88.

Scurlock JMO, Hall DO 1998. The global carbon sink: a grassland perspective. Global Change Biology 4: 229–233.

Silvertown J, Franco M 1993. Plant demography and habitat: a comparative approach. Plant Species Biology 8: 67–73.

Soussana J-F, Loiseau P, Vuichard N, Ceschia E, Balesdent J, Chevallier T, Arrouays D 2004. Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use and Management 20: 219–230.

Sparrow AD, Friedel MH, Tongway DJ 2003. Degradation and recovery processes in arid grazing lands of central Australia Part 3: implications at landscape scale. Journal of Arid Environments 55: 349–360.

Standish R, Sparrow AD, Williams PA, Hobbs R 2009. A state-and-transition model for the recovery of abandoned farmland in New Zealand. In: Hobbs RJ, Suding KN eds New models for ecosystem dynamics and restoration. Washington, DC, Island Press. Pp. 189–205.

Su YZ, Zhao HL, Zhang TH 2003. Influences of grazing and exclosure on carbon sequestration in degraded sandy grassland, Inner Mongolia, north China. New Zealand Journal of Agricultural Research 46: 321–328.

Tanentzap AJ, Burrows LE, Lee WG, Nugent G, Maxwell JM, Coomes DA 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. Journal of Applied Ecology 46: 1064–1072.

Treskonova M 1991. Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. New Zealand Journal of Ecology 15: 65–78.

Walker S, King N, Monks A, Williams S, Burrows L, Cieraad E, Meurk C, Overton JMcC, Price R, Smale M 2009. Secondary woody vegetation patterns in New Zealand's South Island dryland zone. New Zealand Journal of Botany 47: 367–393.

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH 2008. Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. Proceedings of the National Academy of Sciences (USA)

105: 7676–7680.

Zavaleta ES, Kettley LS 2006. Ecosystem change along a woody invasion chronosequence in a California grassland. Journal of Arid Environments 66: 290–306.