

## ORIGINAL ARTICLE

Agrosystems

# Soil carbon in regenerating high country grassland agroecosystems in New Zealand

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## Abstract

Pastoral grasslands in New Zealand's mountainous landscapes contribute substantially to a primarily agricultural national economy. This landscape supports mosaics of regenerating indigenous biodiversity among more productive naturalized exotic herbage, each raising fundamental ecological, agronomic, and environmental concerns. Our objective was to investigate whether increased or lesser attention to native plant assemblages in these vegetation mosaics significantly influences soil carbon (C) stocks. At mid-altitudes below the original tree line, we compared paired plots of regenerating successional endemic myrtaceous woody shrub communities (*Kunzea ericoides*, kānuka) with exotic pasture at comparable slopes and aspects. We also investigated native snow tussock grass communities, the dominant vegetation at higher altitudes bordering the original tree line. Soils beneath kānuka had significantly higher C concentrations, C stocks, and carbon:nitrogen (N) ratios than adjacent areas of pasture. Soil C stocks were 15.43% higher under kānuka than under adjacent pasture. The bases of snow tussocks were frequently raised 10–20 cm above the surrounding inter-tussock land surface with a sparse vegetation cover that provides pathways for stock, making them more susceptible to soil erosion. Soil directly beneath the snow tussocks had significantly higher C, nitrogen, and phosphorus (P) in comparison with adjacent inter-tussock spaces. Soil C stocks were 38.7% higher under snow tussock than in the adjacent inter-tussock spaces. Our findings indicate that maintaining and enhancing endemic woody shrub and snow tussock assemblages is beneficial to productive and sustainable pasturage, while also playing a significant role in biodiversity conservation and climate change mitigation.

## Plain Language Summary

Mountain grasslands in New Zealand contain some of the original native plants from before pasture was established using more productive species from the northern hemisphere. We wanted to know if the presence of either a naturally

**Abbreviations:** BD, bulk density; CC, Cameron Creek; HC, Hospital Creek; LC, Lagoon Creek.

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regenerating native shrub or endemic tall tussock grasses affects the amount of carbon stored in the soil of this sheep-grazed landscape. Our results showed that soil beneath both types of native vegetation stored more carbon and more plant nutrients. Although sheep urine and feces on trodden pathways between the taller native vegetation might be expected to have the opposite effect, their trodden pathways are more susceptible to soil loss through wind and rainfall. We concluded that the presence of native plants plays an important role through increased storage of carbon in soil, benefiting climate change mitigation. Their presence in the grassland vegetation also contributes to biodiversity conservation and sustainable agriculture practices.

## 1 | INTRODUCTION

Over one-third of New Zealand is referred to as “high country”; it is mostly steeply sloping land at altitudes of 400–1000 m a.s.l. beneath the original upper limit of forest growth (the tree line) and bordering the lower limit of the alpine zone (McGlone, 1989). Management of this landscape attempts to balance the combined interests of farming, conservation, hunting, and recreation (A. L. Brower et al., 2020; O’Connor, 2003; Rissman et al., 2021). In addition to protected conservation estate at higher altitudes, approximately half of the high country has been maintained as pastoral farmland since the original forests were lost through an historic sequence of fire, logging, and later conversion to sheep- and cattle-grazed pasture (Thom, 2016; Wardle, 1991). These agrosystems support most of New Zealand’s nonirrigated pastoral agriculture as well as 28% of the country’s native biodiversity, 90% of which is endemic and found nowhere else (Mark, 2021).

Following forest depletion below the alpine zone, indigenous tussock grasslands extended their range to lower altitudes together with many native species of flora and fauna (Tozer et al., 2021). Subsequently, tussock grasslands below the original tree line have been extensively modified and depleted through liming, fertilization, over-sowing with more productive exotic grasses and legumes, weed invasion, and grazing by stock and several species of wild ungulates, marsupials, and rodents (Duncan et al., 2001; Sage et al., 2009; Scott et al., 2001). The dynamics of the current mosaic of native and exotic vegetation create management challenges with consequences for farming, conservation, and environment. This includes both protection and building of soils (Hewitt et al., 1998; Rumpel et al., 2018; Whitehead, 2020). The impacts on soil organic matter are of special concern in these environments because of its key role in increasing soil fertility and reducing erosion (Lal, 2004).

New Zealand soils already support moderate to high carbon (C) stocks, but it has been suggested that agronomic management practices may facilitate additional gains in the high country (L. A. Schipper et al., 2010; Whitehead et al., 2018).

In view of the large extent of this landscape, fractionally small increments in C storage have the potential for a large contribution toward climate change mitigation (Amundson et al., 2015; Smith, 2008). However, both increases and decreases in soil C have been previously reported in New Zealand and elsewhere when investigating the effects of woody revegetation or encroachment of trees into areas of pasture grassland (Tate, Scott, Parshotam, et al., 2000; Tate, Scott, Ross, et al., 2000; Byers et al., 2024; Davis & Condron, 2002; Guidi et al., 2014; Paul et al., 2002; Poeplau & Don, 2013; L. A. Schipper et al., 2017; Stockmann et al., 2013).

Our hypothesis is that the enhancement of patches of woody shrub communities and less productive snow tussocks within pasturage could increase soil C sequestration. The objective of this study was to investigate spatial variation of soil C within the diverse landscape mosaic of a high country sheep station by (i) comparing regenerating mid-altitude shrubland with adjacent pasture and (ii) investigating smaller scale differences within higher altitude tussock grassland. Completion of these two objectives will expand current understanding around differences in soil C stocks between grassland and native shrub/tussock environments in mid- to high-altitude agricultural systems.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

#### 2.1.1 | Location and history

This research was based at Mt. Grand Station, a 1600 ha high country pastoral farm at Hawea, Central Otago, in the South Island of New Zealand. The station consists mainly of steep hill country (400–1445 m a.s.l.) across three watershed catchments; 60% is above 1000 m, with 94% of the land considered suitable for grazing. Vegetation cover, plant communities, and productivity are substantially associated with altitude and aspect of the land (Duncan et al., 2001).

Summer soil moisture deficits (annual rainfall is 690–800 mm) constrain pasture production to overall yields of approximately 3 t ha<sup>-1</sup> (Richard Lucas, personal communication, 2024). Soils in this region have been created from schist, loess, and alluvial gravels and are prone to erosion by wind and water, especially after the loss of vegetation through overgrazing or fire (Molloy, 1998). High country soils naturally have low pH and low fertility, particularly in terms of phosphorus, sulfur (S), molybdenum (Mo), and boron (B) (Hendrie et al., 2021) as reflected at Mt. Grand (Zhang et al., 2022a).

European settlers in the 1850s were the first to farm in the area, but increased burning, high stocking rates, and introduction of rabbits led to the replacement of snow tussock with a sparser short-tussock grassland. Overgrazing by sheep and rabbits typified much of the high country until the mid-1900s when serious concerns of desertification, soil erosion, and lost production became apparent. Subsequently, vegetation cover at Mt. Grand increased from a “very depleted state” in the early 1900s through better management, which changed a “once desert-like landscape into a relatively high producing unit within 30 years from 1944” (Provost, 2024). Changed farm management included aerial fertilizer dressing and over-sowing with exotic grasses and legumes, combined with better grazing practices and control of rabbits. The station currently runs approximately 4000 stock units of Merino sheep with a small number of cattle. At present, Mt. Grand is a Lincoln University-owned farm.

## 2.1.2 | Vegetation and agrosystem

Vegetation across the station varies with altitude, aspect, and slope within the three different catchments (Figure 1). At lower altitudes, where there is better access to farm machinery, more attention is given to fertilization and higher yielding pasture with little native vegetation apart from in gullies alongside waterways and rock exposures in limited locations inaccessible to stock. At mid-altitudes (approx. 480–820 m), vegetation is more diverse in less-productive grassland largely comprising of exotic grasses, clovers, and other herbs, with areas of invasive naturally regenerating woody shrubs at different levels of abundance across the station. In particular, regenerating patches of varying sizes of a myrtaceous shrub (*Kunzea ericoides*, kānuka) are naturally common and widespread across the landscape at Mt. Grand. Toward the upper part of this altitudinal range, native tussock grasses (*Chionochloa* spp.) become a dominant feature of the vegetation, extending into the alpine zone.

The three different watershed catchments across the station have variable stocking rates of sheep, with a range of 0.32–1.79 stock units ha<sup>-1</sup> annum<sup>-1</sup>, managed by rotational grazing across approximately 15 different-sized blocks of land sepa-

### Core Ideas

- Mountainous New Zealand landscapes support mosaics of native vegetation within predominantly exotic naturalized grassland.
- We hypothesize that soil carbon is enhanced by endemic woody shrub and snow tussock assemblages within pasturage.
- Our findings indicate a significant role for indigenous biodiversity through building and protecting soils.
- Endemic shrubs and tussocks within derived high country grasslands are beneficial for agrosystems and environment.

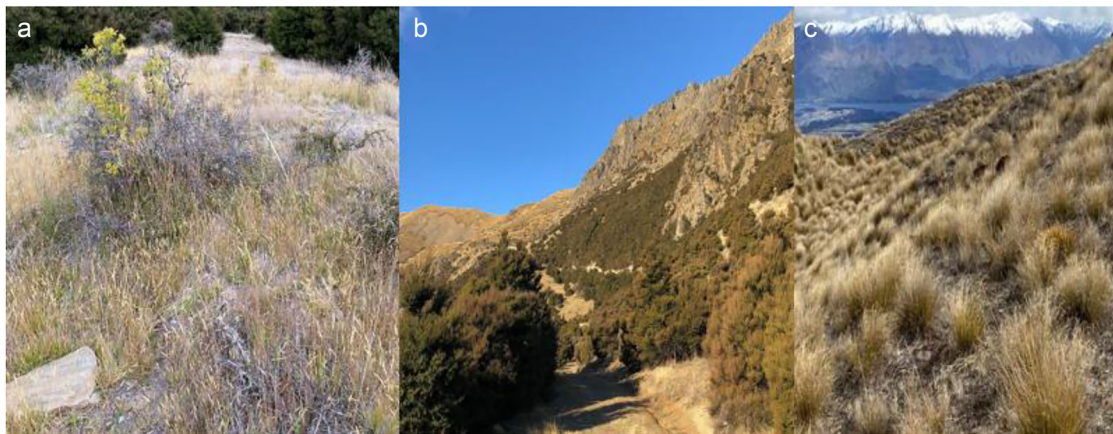
rated by fencing. Stocking rates are determined by vegetation assemblages and productivity. Rabbits, deer, pigs, and other species of ungulates, all of which were introduced into New Zealand, range across the station aside from limited success with their control, usually by shooting and hunting. Aerial fertilizer amendments of superphosphate with sulfur have been applied approximately biennially to sample sites at a rate of 150 kg ha<sup>-1</sup>. Lagoon Creek (LC) sites have not been used for farming or received fertilizer since the station went through Tenure Review (A. Brower, 2008) in 2016, when ownership transferred to the Department of Conservation.

## 2.2 | Sampling strategy

Sampling at mid-altitude locations was undertaken in both mid-winter (June 2019) and mid-summer (January 2020). Sampling at higher altitude locations was undertaken in both mid-summer (January 2020) and early spring (September 2020), during several sampling trips.

### 2.2.1 | Mid-altitude sites

ArcGIS was used to identify potential areas of well-established kānuka and adjacent areas of exotic grassland pasture and assess the altitude, slope, and aspect of each area; the latter two factors have been linked to changes in soil C in high country environments (Mackay et al., 2018), while changes in soil moisture and temperature with altitude can also affect soil C dynamics (Griffiths et al., 2009). These areas were then visited in person to confirm the remote sensing observations. Final site selection was largely based on safe accessibility on foot and proximity to access roads. At mid-altitudes (480–820 m), reasonably accessible sam-



**FIGURE 1** Representative vegetation communities at Mt. Grand Station. (a) Mid-altitude site with exotic pasture grass (*Anthoxanthum odoratum*), clumps of native shrub (*Discaria toumatou*, matagouri), an invasive shrub (*Rosa rubiginosa*, sweet briar), and a stand of native *Kunzea ericoides* (kānuka) visible in the background. (b) Regenerating kānuka, with upper range approximating to the original tree line, with rocky outcrops of exposed schist and sub-alpine vegetation cover in the background. (c) Snow tussock (*Chionochloa* spp.) communities at higher altitudes, with spaces between tussocks comprising of exposed soil generally with a sparse groundcover of prostrate endemic shrubs and herbs, and invasive exotic species (especially *Hieracium* spp., *Trifolium repens*, and *Lotus pedunculatus*). Lake Wānaka and the alpine zone are visible in the background of the photograph.

pling locations were located in each of the three different catchments (Table 1). These provided paired comparisons of the two different predominant types of vegetation cover (kānuka and mixed pasture grassland, Figure 1) where the differences in altitude (0–40 m), slope (0–10°), and aspect (0–22.5°) between the paired sites were minimized. Historical aerial photographs indicated the kānuka stands had been established prior to the 1980s. Although this species has some fire resilience, there are no records of burning to suggest this is longer established vegetation. The height of the near-closed canopies varied between 2 and 5 m, precluding any other significant ground cover, in patches approximately 100–500 m<sup>2</sup>. Sample sites were labeled using a two-part system: the first part is the initials of the catchment of interest (CC, HC, and LC, for Cameron Creek, Hospital Creek, and Lagoon Creek, respectively), while the second part indicates the vegetation type (PG and K for pasture grass and kanuka, respectively). For example, the CC pasture grass and CC kānuka sampling sites were named CCPG and CCK, respectively. A numeral was added to the end of the site label when more than one site with a given catchment-vegetation type combination was analyzed. All sample sites and their abbreviations are identified in Table 1.

At each sampling location in both kānuka and pasture, 17 soil samples were collected (0- to 15-cm depth) using a 5.4-cm diameter cylindrical steel auger with 1-cm cutting edge blades. The 17 samples were collected from two perpendicular 18 m × 18 m transects, with their centers intersecting in the shape of a cross, with each sample taken 2.25 m apart. Adjacent pairs of samples were subsequently bulked, apart from the sample at the intersection of the transects, thus providing

nine pseudo-replicate samples from every sampling location. More detailed sample site descriptions for pasture grass and kānuka are provided in Table 1.

### 2.2.2 | Higher altitude sites

In the second part of the study, focusing on native snow tussock communities at higher altitudes (approximately 800–1000 m), both above and below the original tree line, sampling sites were selected to include typical tussock grassland vegetation assemblages, with final site selection largely based on safe accessibility on foot and proximity to access roads for the collection and transportation of samples. Description of tussock sampling sites is provided in Table 2. To provide paired comparisons, soil immediately beneath grassland tussocks was compared with soil in adjacent inter-tussock spaces that contained only a sparse groundcover of prostrate endemic shrubs and herbs, frequently with exotic invasive herbaceous plants or surrounded by bare soil (Figure 1). The same auger as described above was drilled through the center of each tussock, retaining soil at a depth of 15 cm below its first appearance.

## 2.3 | Sample and data analysis

### 2.3.1 | Soil analyses

Soil samples were stored in polythene bags in a cooler bin and transported to Lincoln University within 48 h. Samples were weighed and air-dried at 28°C for a minimum

TABLE 1 Location and description of mid-altitude mixed pasture and kānuka sample sites, vegetation, and soils.

Catchment	Location	Altitude	Aspect	Slope	Vegetation	Soil texture	Bulk density	pH	
								Winter	Summer
Cameron Creek pasture grass (CCPG)	169°19'34" E 44°37'57" S	620 m	North-west	20–30°	Higher producing pasture with full sward cover <sup>1, 2, 3, 4</sup> .	% Clay = 1.31 % Silt = 75.46 % Sand = 23.23	1.02	5.06	5.13
Cameron Creek kānuka (CCK)	169°19'35" E 44°38' S	647 m	North-west	20–30°	Smaller area of dense regenerating kānuka growth, well established leaf litter layer.	% Clay = 1.59 % Silt = 67.72 % Sand = 30.69	0.99	4.74	4.39
Hospital Creek pasture grass (HCPG)	169°19'5" E 44°39'6" S	480 m	North-west	30–40°	Lower producing pasture with sparse sward cover <sup>2, 5, 6, 7, 8, 9, 10, 11, 12, 13</sup> .	% Clay = 0.74 % Silt = 64.31 % Sand = 34.95	1.07	5.46	5.50
Hospital Creek kānuka (HCK)	169°19'16" E 44°39'7" S	480 m	North	30–40°	Less dense kānuka growth, sparse litter layer.	% Clay = 0.87 % Silt = 62.62 % Sand = 36.51	0.87	5.28	5.23
Lagoon Creek pasture grass (LCPG)	169°20'22" E 44°40'10" S	810 m	North-west	40–50°	Lower producing pasture, no stock <sup>5, 7, 9, 14, 15, 16, 17, 18, 19</sup> .	% Clay = 1.27 % Silt = 73.69 % Sand = 25.04	0.92	5.60	5.48
Lagoon Creek kānuka 1 (LCK1)	169°20'36" E 44°40'2" S	770 m	North-west	30–40°	Dense area of well-established kānuka growth and leaf litter layer. Stock have been removed.	% Clay = 0.93 % Silt = 50.03 % Sand = 49.04	0.8	5.05	5.11
Lagoon Creek kānuka 2 (LCK2)	169°20'34" E 44°40'7" S	820 m	North-west	30–40°	Dense area of well-established kānuka growth and leaf litter layer. Stock have been removed.	% Clay = 0.73 % Silt = 65.56 % Sand = 33.71	1	5.42	5.09

Note: Dominant plant community assemblages: *Lolium perenne*<sup>1</sup>, *Dactylis glomerata*<sup>2</sup>, *Poa pratensis*<sup>3</sup>, *Trifolium subterraneum*<sup>4</sup>, *Agrostis capillaris*<sup>5</sup>, *Bromus diandrus*<sup>7</sup>, *Bromus hordeaceus*<sup>8</sup>, *Trifolium glomeratum*<sup>9</sup>, *Trifolium striatum*<sup>10</sup>, *Cynosurus cristatus*<sup>11</sup>, *Anothoxanthum odoratum*<sup>12</sup>, *Rumex acetosella*<sup>13</sup>, *Bromus mollis*<sup>14</sup>, *Elymus Magallanes*<sup>15</sup>, *Trifolium dubium*<sup>16</sup>, *Trifolium striatum*<sup>17</sup>, *Trifolium arvense*<sup>18</sup>, *Trifolium repens*<sup>19</sup>.



TABLE 2 Location and description of tussock and inter-tussock sample sites, vegetation, and soils.

Site	GPS co-ordinates	Elevation	Aspect	Slope	Vegetation	Soil texture	Bulk density	pH											
								T	IT										
Tussock 1	169°21'36" E 44°39'35" S	1140 m	East	20–30°	<i>Chionochloa rigida</i> , <i>Chionochloa rigida</i> + <i>Chionochloa macra</i> hybrid, <i>Poa colenso</i>	% Clay = 1.41 % Silt = 68.41 % Sand = 30.18	T = 0.46 IT = 0.62	4.50	4.93										
										Tussock 2	169°20'46" E 44°38'8" S	1140 m	North	20–30°	<i>Chionochloa rigida</i> , <i>Chionochloa rigida</i> + <i>Chionochloa macra</i> hybrid	% Clay = 1.47 % Silt = 70.27 % Sand = 28.26	T = 0.61 IT = 0.81	4.44	4.77
Tussock 4	169°21'50" E 44°38'47" S	1333 m	North	20–30°	<i>Chionochloa macra</i> , <i>Festuca</i> <i>mathewsii</i>	% Clay = 1.19 % Silt = 62.94 % Sand = 35.87	IT = 0.63	–	5.21										
										Tussock 5 (near T1)	169°20'54" E 44°39'36" S	1145 m	South-west	10–20°	<i>Chionochloa rigida</i> , <i>Chionochloa rigida</i> + <i>Chionochloa macra</i> hybrid, <i>Poa colenso</i>	% Clay = 1.02 % Silt = 69.32 % Sand = 29.65	T = 0.73 IT = 0.79	4.70	5.15
Tussock 6 (near T2)	169°20'54" E 44°38'24" S	1245 m	North-west	30–40°	<i>Chionochloa rigida</i> , <i>Chionochloa rigida</i> + <i>Chionochloa macra</i> hybrid	% Clay = 0.86 % Silt = 64.62 % Sand = 34.53	T = 0.49 IT = 0.60	4.54	4.84										
										Tussock 7	169°19'49" E 44°38'22" S	967 m	Northwest	20–30°	<i>Chionochloa rigida</i>	% Clay = 0.97 % Silt = 67.27 % Sand = 31.76	T = 0.66 IT = 0.66	4.99	5.16

Note: T and IT represent tussock and inter-tussock, respectively.

of 96 h and then crushed and sieved (<2 mm) prior to analysis. Total C and nitrogen (TN) were determined using an Elementar Vario-Max CN Elemental Analyzer (Elementar). Other macronutrients and trace element concentrations were determined at Lincoln University Analytical Services using a Varian 720-ES Inductively Coupled Plasma Optical Emission Spectrometer fitted with an SPS-3 auto-sampler and ultrasonic nebulizer (Varian IC) following microwave digestion of samples in  $\text{HNO}_3\text{-H}_2\text{O}_2$  (Simmler et al., 2013). Soil pH was measured using a soil:deionized water ratio of 1:2.5 (w/v) (Rayment & Lyons, 2011).

At each sample site, three additional samples had been collected at a random selection of sampling locations to provide samples for bulk density (BD) and texture analysis. These were collected to a depth of 16.5 cm using a 5.4-cm diameter bucket auger (378 mL). Sample material (rocks and plant debris) that was removed from the sieve (>2 mm) during the air-drying process for each sample was stored to be volumetrically measured later using a standard water displacement method. The retained material was then added to water stored in a volumetric measuring flask, measuring the displacement to calculate the volume of material >2 mm contained in each sample. The air-dried samples were then placed into a 105°C-degree oven for 8–24 h, before being placed into a desiccator, then weighed on a balance, and the oven-dry weight recorded. Soil texture was analyzed using laser diffraction (Malvern Mastersizer 2000; Malvern Panalytical Ltd.), after pretreatment with sodium dithionite and hydrogen peroxide to remove iron oxides and organic matter (Gee & Orr, 2002; Ryzak & Bieganski, 2011).

### 2.3.2 | Carbon stocks

Soil C stocks were calculated to a fixed depth as the product of soil BD, sample depth, and C concentration. The stocks were also estimated using an equivalent soil mass (ESM) approach, where the fixed-depth soil C stocks at the site with the higher soil mass in the 0- to 16.5-cm depth range (i.e., higher BD) were normalized to the soil mass on the neighboring paired sample in each case (typically the pasture and inter-tussock sites had the higher BD). This was done to account for the differences in BD under the different land uses (Wendt & Hauser, 2013).

### 2.3.3 | Statistics

Differences between soils from adjacent paired vegetation types within catchments were analyzed using two-sample *t*-tests or one-way analysis of variance; the latter was also used to compare sites across catchments. When differences were significant, Tukey's honestly significant difference post-hoc test was used to identify differences between groups. Differ-

ences between means were analyzed using the Kruskal–Wallis test when the requirements of normality and homoscedasticity for parametric tests could not be met (see below); here Dunn's test was used for multiple comparisons. Complete datasets for each season were analyzed using linear mixed-effects models fitted with restricted maximum likelihood to test whether season and vegetation type significantly affected the response variables, while accounting for random variation associated with site-specific characteristics (slope, aspect, and elevation). Normality and homoscedasticity of the residuals were confirmed by visual assessment of residual plots and plots of predicted versus observed values. Where these conditions were not met, either  $\log_{10}$  or Box-Cox transformations were used to fulfill the test requirements. All statistical analyses were carried out using Minitab (Version 22.1, 2024 Minitab, LLC) and significance was assumed at *p*-value < 0.05.

## 3 | RESULTS

### 3.1 | Mid-altitude sites

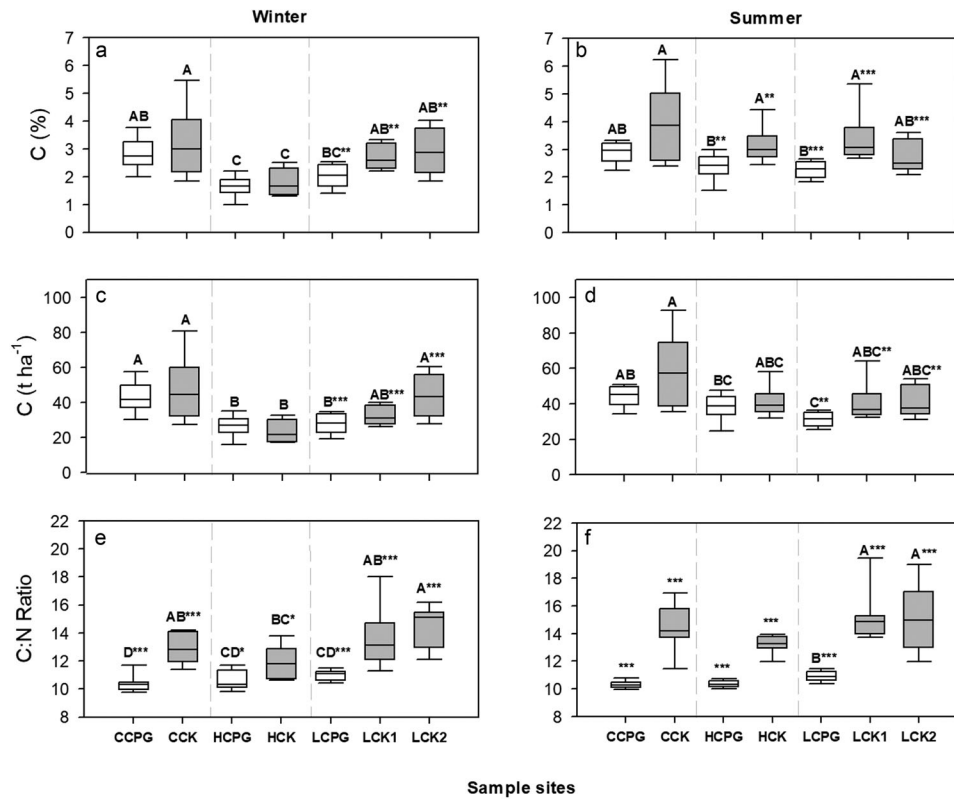
#### 3.1.1 | Soil carbon

The range of soil C concentrations was 1.8%–3.9% (mean 2.98%), with C stocks of 23.5–57.8 t ha<sup>-1</sup> (mean 41.1 t ha<sup>-1</sup>). On an individual site basis, higher soil C concentrations were sometimes evident beneath kānuka vegetation compared to adjacent areas of mixed pasture grass (Figure 2). Differences were more pronounced in summer, with significant differences between the vegetation communities in two of the catchments. When all three catchments and both seasons were considered together, significant differences in soil C concentrations were found to be associated with vegetation (*p*-value = 0.001) and season (*p*-value ≤ 0.001). The highest mean C concentration (3.9%) was recorded under kānuka in the summer, and the lowest (1.8%) was under pasture grass in the winter.

Kānuka stands also had generally higher soil C stocks than pasture (Figure 2). Analysis of the combined dataset across the three different catchments showed that areas of kānuka had significantly higher soil C concentrations than areas of mixed pasture (mean difference 24%; *p*-value < 0.001), while the corresponding difference between soil C stocks was 8.2% (fixed depth, 15.4% for ESM) (*p*-value = 0.029). Bulk density tended to be higher under pasture, which resulted in soil C stocks at pasture sites decreasing when stocks were calculated using ESM (Table 3).

#### 3.1.2 | Carbon:nitrogen ratio

The complete dataset showed that soil C:N varied significantly under different vegetation types (*p*-value ≤ 0.001) and



**FIGURE 2** Winter (a, c, and e) and summer (b, d, and f) seasonal sampling of soil (0- to 15-cm sample depth) carbon concentrations (%) (a and b), carbon stocks ( $\text{t ha}^{-1}$ ) (c and d), and carbon to nitrogen ratio (e and f) for three independent mixed pasture (PG, white boxes) and kākūka (K, shaded boxes) paired site comparisons [indicated by lines on chart]. Sites Cameron Creek (CC), Hospital Creek (HC), and Lagoon Creek (LC) are located in different stream catchments. Samples ( $n = 9$ ) were collected in June 2019 (winter) and January 2020 (summer). Means that do not share a letter were significantly different ( $p$ -value  $< 0.05$ ). The summer data for C:N ratio (f) were analyzed using a nonparametric test and only sites in each catchment were compared. Asterisks represent a significant difference recorded for paired site comparisons within catchments, where \* $p$ -value  $\leq 0.05$ , \*\* $p$ -value  $\leq 0.01$ , and \*\*\* $p$ -value  $\leq 0.001$ . The upper whisker represents the maximum, the upper edge of the box represents quartile 3, the middle of the box represents the median, the lower edge of the box represents quartile 1, and the lower whisker represents the minimum.

seasons ( $p$ -value = 0.002), with higher C:N ratios in kākūka soils than the mixed pasture grass soils (Figure 2). The largest difference in C:N ratio between the two vegetation communities was observed comparing LCPG and LCK2 in summer, where an additional 4.32 units of C:N under kākūka was recorded.

### 3.1.3 | Nitrogen and phosphorus

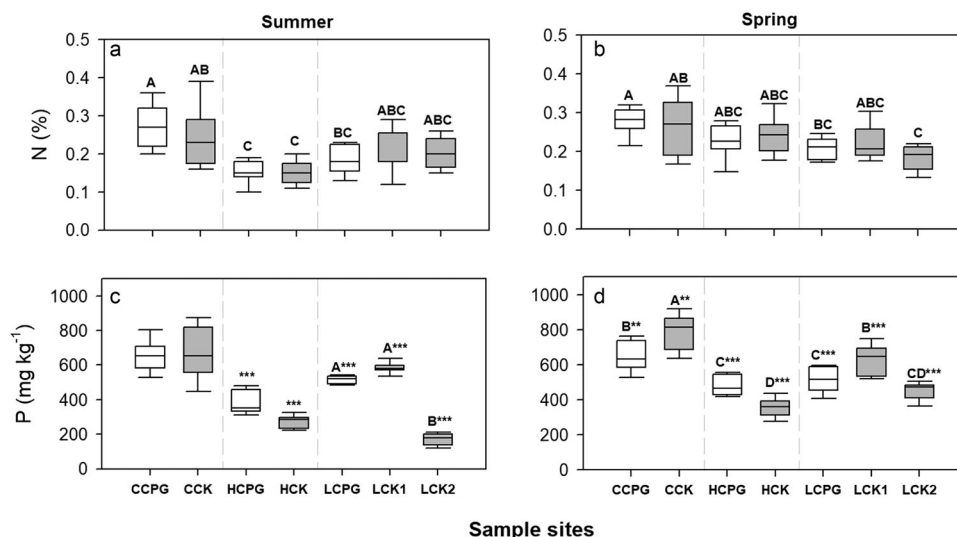
While the highest mean TN concentration of 0.28% was recorded under pasture grass during summer, and the lowest under kākūka during winter (0.15%), the complete dataset only showed significant seasonal differences in TN concentrations ( $p$ -value  $< 0.001$ ), but not between vegetation types ( $p$ -value = 0.748) (Figure 3). The combined dataset for total phosphorus (TP) also showed that vegetation and season ( $p$ -value  $< 0.005$ ) both had significant effects with higher mean TP concentrations under pasture grass of  $532 \text{ mg kg}^{-1}$  (95% confidence intervals [CI] [501, 563]) than under kākūka,

where the mean was  $492 \text{ mg kg}^{-1}$  (CI [441, 541]). Soil TP was similarly variable between winter and summer sampling, with mean concentrations of  $464 \text{ mg kg}^{-1}$  (CI [416, 512]) and  $554 \text{ mg kg}^{-1}$  (CI [516, 592]), respectively.

## 3.2 | Higher altitude tussock grassland

### 3.2.1 | Soil carbon

Both the seasonal and complete datasets showed that vegetation had a significant effect on soil C concentrations and stocks ( $p$ -value  $\leq 0.001$ ), while seasonal differences were not significant for either ( $p$ -value  $> 0.566$ ). Mean soil C concentrations in the summer were higher under tussock (5.30%; CI [5.00, 5.60]) than adjacent inter-tussock spaces (3.04%; CI [2.78, 3.31]) (Figure 4). This pattern was the same in the spring, where mean C concentrations underneath tussock (3.96%; CI [3.60, 4.32]) were higher than in the inter-tussock spaces (2.96%; CI [2.60, 3.32]).



**FIGURE 3** Winter (a and c) and summer (b and d) seasonal sampling of soil (0- to 15-cm sample depth) nitrogen (%) (a and b) and phosphorus concentrations ( $\text{mg kg}^{-1}$ ) (c and d) for three independent mixed pasture (PG, white boxes) and kānuka (K, shaded boxes) paired site comparisons (indicated by lines on chart). Sites Cameron Creek (CC), Hospital Creek (HC), and Lagoon Creek (LC) are located in different stream catchments. Samples ( $n = 9$ ) were collected in June 2019 (winter) and January 2020 (summer). Means that do not share a letter were significantly different ( $p$ -value  $< 0.05$ ). The summer data for P (c) were analyzed using a nonparametric test and only sites in each catchment were compared. Asterisks represent a significant difference recorded for paired site comparisons within catchments, where  $**p$ -value  $\leq 0.01$  and  $***p$ -value  $\leq 0.001$ . The upper whisker represents the maximum, the upper edge of the box represents quartile 3, the middle of the box represents the median, the lower edge of the box represents quartile 1, and the lower whisker represents the minimum.

Mean soil C stocks in the summer beneath tussocks were  $10.26 \text{ t ha}^{-1}$  (CI [5.82, 14.7]) higher than in adjacent inter-tussock spaces, with significant pairwise differences between all three sites (Table 4; Figure 4). In the spring, while the between-site comparisons did not reveal any significant differences, the overall mean soil C stock in the tussock samples ( $36.05 \text{ t ha}^{-1}$ ; CI [33.03, 39.29]) was significantly greater than in the inter-tussock spaces ( $29.74 \text{ t ha}^{-1}$ ; CI [27.29, 32.41]) ( $p$ -value = 0.003).

### 3.2.2 | Carbon-to-nitrogen ratio

Soil beneath tussocks consistently had a higher mean C:N ratio compared to inter-tussock spaces (Figure 4). Here, the combined dataset showed that vegetation had a significant effect on the ratio ( $p$ -value  $\leq 0.001$ ), but season did not ( $p$ -value = 0.364). The largest difference was observed at Site T6 during spring, when an additional 7.0 units of C:N were recorded below tussocks.

### 3.2.3 | Nitrogen and phosphorus

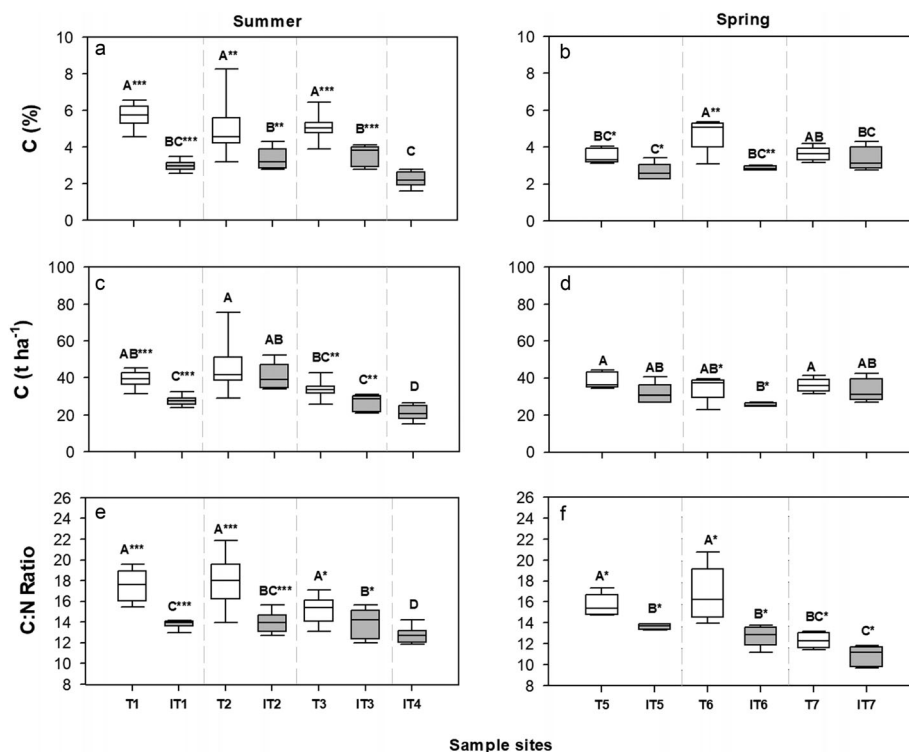
The complete dataset showed that only vegetation had a significant effect on soil TN and TP concentrations ( $p$ -value  $< 0.001$ ). There were significantly higher soil TN concentrations beneath tussocks than inter-tussock spaces

during summer (Figure 5), with equivalent values at the fourth set of inter-tussock samples. No significant differences were recorded during spring. The highest mean TN concentration of 0.32% and the lowest concentration of 0.19% were both recorded in inter-tussock spaces in spring.

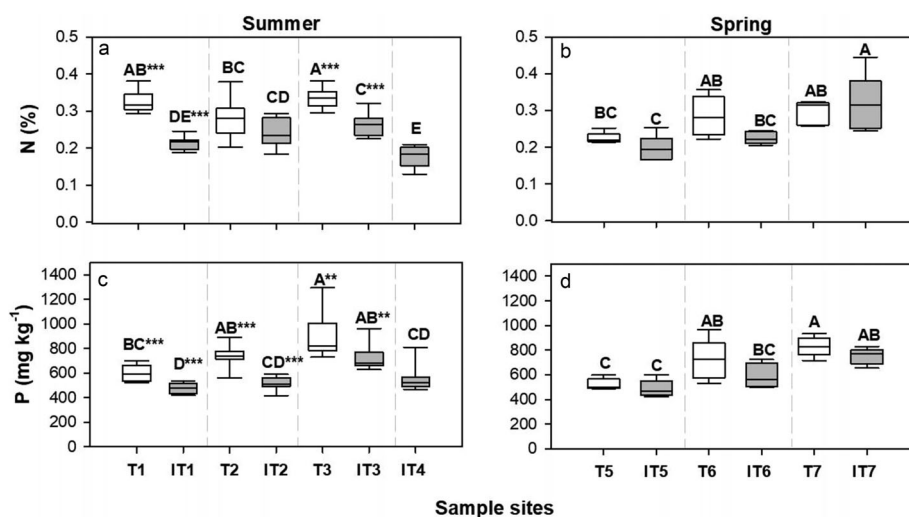
## 4 | DISCUSSION

### 4.1 | Mid-altitude woody shrub and pasture

Soil C results comparing mixed pasture with kānuka indicate some potential for kānuka to enhance C sequestration at low to mid-altitudes. Short-term seasonal variations can be explained by differing biological and environmental conditions (Schmidt et al., 2011; Schipper et al., 2017; Lambie & Dando, 2020). Soil C concentrations and stocks are marginally lower but similar to findings of earlier research in different parts of New Zealand; 4.2%–7.3% (Hedley et al., 2013) and  $91$ – $111 \text{ t ha}^{-1}$  (Scott et al., 2000). Two studies that re-sampled areas of regenerating hill country pasture from various locations across New Zealand, without distinguishing differences between shrubland and pasture, recorded increases in soil C stocks of  $0.6 \text{ t C ha}^{-1} \text{ year}^{-1}$  (Schipper et al., 2014), undoubtedly reflecting wider adoption of better agronomic practices and rabbit control in the high country, as described above at Mt. Grand.



**FIGURE 4** Summer (a, c, and e) and spring [b, d, and f] sampling of soil (0- to 15-cm sample depth): carbon concentrations (%) (a and b), carbon stocks (t ha<sup>-1</sup>) (c and d), and carbon to nitrogen ratio (e and f) for three independent tussock (T, open boxes) and inter-tussock (IT, shaded boxes) paired site comparisons (indicated by lines on chart). Only inter-tussock samples were collected at sample site 4 during the initial summer sampling. Samples were collected in January (summer,  $n = 10$ ) 2020 and September (spring,  $n = 5$ ) 2020. Means that do not share a letter were significantly different ( $p$ -value  $< 0.05$ ). Asterisks represent a significant difference recorded for paired site comparisons, where \* $p$ -value  $\leq 0.05$ , \*\* $p$ -value  $\leq 0.01$ , and \*\*\* $p$ -value  $\leq 0.001$ . The upper whisker represents the maximum, the upper edge of the box represents quartile 3, the middle of the box represents the median, the lower edge of the box represents quartile 1, and the lower whisker represents the minimum.



**FIGURE 5** Summer (a and c) and spring (b and d) seasonal sampling of soil (0- to 15-cm sample depth) nitrogen (%) (a and b) and phosphorus concentrations (mg kg<sup>-1</sup>) (c and d) for three independent tussock (T, white boxes) and inter-tussock (IT, shaded boxes) paired site comparisons (indicated by lines on chart). Only inter-tussock samples were collected at sample site 4 during the initial summer sampling. Samples were collected in January (summer,  $n = 10$ ) 2020 and September (spring,  $n = 5$ ) 2020. Means that do not share a letter were significantly different ( $p$ -value  $< 0.05$ ). Asterisks indicate where a significant difference was recorded for the paired vegetation comparisons, with \* $p$ -value  $\leq 0.05$ , \*\* $p$ -value  $\leq 0.005$ , and \*\*\* $p$ -value  $\leq 0.001$ . The upper whisker represents the maximum, the upper edge of the box represents quartile 3, the middle of the box represents the median, the lower edge of the box represents quartile 1, and the lower whisker represents the minimum.

**TABLE 3** Soil carbon stocks at pasture and kānuka sites, calculated using fixed depth and equivalent soil mass.

Site	Season	Soil C stocks—Bulk density calculation (t ha <sup>-1</sup> )	Soil C stocks—Equivalent soil mass calculation (t ha <sup>-1</sup> )
CCPG	Winter	43.04	41.84
CCK		46.8	X
HCPG		26.36	21.53
HCK		23.45	X
LCPG		27.94	24.38
LCK1		32.27	X
LCK2		44.32	35.61
CCPG	Summer	44.10	42.87
CCK		57.83	X
HCPG		38.48	31.43
HCK		41.53	X
LCPG		31.35	27.36
LCK1		40.58	X
LCK2		41.9	33.67

Note: X represents paired sample site with lower bulk density and no equivalent soil mass calculation required. Site descriptions are provided in Table 1.

Abbreviations: CCK, Cameron Creek kānuka; CCPG, Cameron Creek pasture grass; HCK, Hospital Creek kānuka; HCPG, Hospital Creek pasture grass; LCK, Lagoon Creek kānuka; LCPG, Lagoon Creek pasture grass.

Climate change mitigation policy in New Zealand is substantially reliant on afforestation with exotic conifers, particularly on existing high country grasslands, but there is uncertainty around its effects on soil C stocks. One study, for example, reported initially reduced soil C of 4.5 t ha<sup>-1</sup>, but no difference after 20 years (Davis & Condon, 2002). Plantation forests also have negative effects on native biodiversity and increased fire risk (McGregor et al., 2012; Franzese et al., 2017; Nuñez et al., 2017; Taylor et al., 2017; Peltzer, 2018; Wyse et al., 2019). In comparison, revegetation of kānuka in areas of pasture that are environmentally marginal for farming provides a viable option to sequester C, while also providing additional benefits for biodiversity. Accumulation of C in biomass of kānuka is initially slow, but it has been demonstrated that after 55 years, comparable biomass C stocks to exotic plantation forests can be achieved (Scott et al., 2000; Trotter et al., 2005). Aerial photographs show that the shrublands targeted for sampling in the present study have been established for at least 40 years.

The CC catchment at Mt. Grand is a more fertile and productive farming area in comparison with sampling areas in the

**TABLE 4** Mean soil carbon stocks at tussock and inter-tussock sites, calculated using fixed depth and equivalent soil mass.

Site	Season	Soil C stocks (bulk density calculation, t ha <sup>-1</sup> )	Soil C stocks (equivalent soil mass calculation, t ha <sup>-1</sup> )
T1	Summer	39.22	X
IT1		27.72	20.50
T2		45.42	X
IT2		40.70	30.76
T3		33.65	X
IT3		27.11	23.58
IT4		21.15	X
T5	Early spring	38.50	X
IT5		31.42	29.04
T6		34.76	X
IT6		25.72	21.01
T7		35.93	X
IT7		33.38	X

Note: X represents paired sample site with lower bulk density and no equivalent soil mass calculation required. Only inter-tussock samples were collected at site 4. T7 and IT7 had equal bulk density, no equivalent soil mass calculation required at this sample site. Site descriptions are provided in Table 2. T and IT represent tussock and inter-tussock, respectively.

other catchments. Higher stocking rates and a higher clover cover in the sward are the likely explanation for higher N % recorded in soil. Higher soil C:N ratios under kānuka vegetation were probably due to substantial leaf litter deposition with low N and woody debris with high lignin content; kānuka typically grows on nutrient-poor soils. Below ground, root biomass and exudation of organic matter into the soil are also likely to have contributed to the soil C stocks. Reduced nitrification rates under kānuka have been reported by Esperschuetz et al. (2017), which they linked to potential nitrification inhibition by exudates released by the plant roots. However, their finding could also be explained by C-rich rhizodeposits promoting microbial biomass formation and the associated sequestration of mineral N (Fisk et al., 2015; Leptin et al., 2021), which would help stabilize the soil C in these soils (Liang et al., 2017). Root biomass and exudates are also important for increasing soil C concentrations under pasture (Whitehead et al., 2024), so the relative importance of above-versus below-ground contributions to the soil C stocks under the two types of vegetation is an interesting avenue for further research.

Variation of soil TP concentrations between different catchments was likely to be due to a combination of differences in aerial fertilizer application and locations of stock. Increased feral pig activity at LC during the second summer of sampling was reflected in observations of substantial ground disturbance and excrement in the kānuka stands.

## 4.2 | Higher altitude tussock grassland

Higher soil C concentrations under snow tussock than in inter-tussock spaces had an overall mean difference of 43.7%. The only exception was the lowest altitude (967 m) sampling site (T7), where more naturalized pastoral grasses and herbaceous plants prominent in the inter-tussock spaces provided the attraction of better forage for sheep. At all the other higher altitude sites, inter-tussock ground cover was occupied by sparse assemblages of native alpine plants, but otherwise bare soil. The variability of soil C stocks beneath snow tussock reflected lower BD than in inter-tussock soils, with less compaction from animal trampling. This is also explained by large quantities of tussock foliage litter in samples that account for calculated C stocks with mean differences of 24.6% and 38.7% (fixed depth and ESM, respectively). Soil C stocks across all tussock sites ranged from 22.8 to 77.7 t ha<sup>-1</sup> (mean 38.4 t ha<sup>-1</sup>), comparable with earlier studies in South Island snow tussock grasslands: 36–49 t ha<sup>-1</sup> (P. McIntosh et al., 1994) and 33–64 t ha<sup>-1</sup> (Li et al., 2019).

Higher soil N and P concentrations beneath snow tussocks than in inter-tussock spaces (mean differences 26.2% and 22.4%, respectively) appear contrary to expectation since stock movement and deposition of feces and urine are almost entirely in inter-tussock spaces. However, despite higher compaction, soil in inter-tussock spaces is much more susceptible to wind erosion, which is known to be a predominant driver of soil loss in the South Island high country (Basher & Matthews, 1993). Undoubtedly, less plant litter is retained in inter-tussock spaces. It is likely that the elevation of snow tussock ground surface above the level of the ground in inter-tussock spaces mitigates soil erosion through receiving wind-blown soil and debris from adjacent inter-tussock spaces, thus enhancing C and nutrient status of the soil beneath.

## 4.3 | Station-wide comparisons

Comparison of soil C concentrations and stocks in the three vegetation communities (i.e., kānuka and pasture grassland at low altitude to mid-altitude, and snow tussock at higher altitudes of the station) focused on samples collected in the summer to eliminate confounding effects from the previously observed differences between sampling times. The

analysis revealed that vegetation had a significant influence on soil C concentrations ( $p$ -value < 0.001), while altitude did not ( $p$ -value = 0.066). The concentrations were higher in tussock soils (5.30%) than under the other vegetation types ( $p$ -value < 0.05) and similar between kānuka and inter-tussock soils (means of 3.31% and 3.04%, respectively;  $p$ -value > 0.05). Concentrations from pasture grassland soils (2.51%) were slightly lower than in the inter-tussock samples ( $p$ -value > 0.05) and significantly lower than in the kānuka or tussock communities ( $p$ -value < 0.05).

Soil C stocks in the summer were highest under kānuka and tussock, with no significant difference between their mean stocks (45.46 and 39.43 t ha<sup>-1</sup>, respectively;  $p$ -value > 0.05). Mean soil C stocks under the kānuka were significantly higher than those in the pasture grassland and inter-tussock samples (37.97 and 29.17 t ha<sup>-1</sup>, respectively;  $p$ -value < 0.05). Differences between mean C stocks under pasture grassland, tussock, or inter-tussock samples (37.98 t ha<sup>-1</sup>) were not significant.

The effects of topographic variables, such as altitude and slope, on soil C concentrations and stocks can be difficult to disentangle from each other, and other influencing physical and biological factors (Weismeier et al., 2019). Moreover, other factors, such as farm management (fertilization and grazing intensity) and environmental factors (soil mineralogy and slope stability), that were not considered have also been shown to be important (Mackay et al., 2018; Weismeier et al., 2019; Whitehead et al., 2024). The narrow ranges of altitudes and slopes considered here (i.e., 340 m elevation difference between the lowest and highest sites in the mid-altitude range and 10° difference in slope angle) and ongoing farm operations are likely to have been among the key confounding factors that limited our ability to make firm conclusions on the influence of topographic factors on soil C dynamics.

## 5 | CONCLUSIONS

Land management practices, policies, and land use changes undoubtedly play a significant role in soil protection (MacLeod & Moller, 2006; Barnett et al., 2014; Byers et al., 2024). The present study indicates that incorporation of regenerating native vegetation into agricultural pasture is likely to promote the persistence of soil C. Through the avoidance of overgrazing and soil erosion, high country pastures have been accumulating C in recent decades, unlike more intensive irrigated grasslands on the lower altitude plains (L. Schipper et al., 2014). Contemporary farm management and increased interest in protection and restoration of native species have provided better protection of steep slopes and watershed outflow gullies that have also led to a high country landscape with more conspicuous native biodiversity (Zhang et al., 2022a, 2022b).

Differences in vegetation cover had more significant effect on soil C storage than altitude. At mid-altitudes, establishment of native woody shrub communities within mixed pasture has beneficial effects on soil C. Higher altitude tussock grasslands have lower productivity and are grazed much less than lower altitude mixed pasture, but they represent a significant component of high country of soil C storage. Snow tussocks appear to play a significant role within the plant communities through protection of soil, capture of wind-blow, and accumulation of C. These findings add weight to recognized arguments for protecting biodiversity at high altitude. Invasive plants, feral mammalian pests, and poorly managed stock grazing can present a threat to these plant communities and may thus negatively affect underlying soil health by impacting soil C storage. The extent to which this can happen in high country ecosystems should be explored further. Ultimately, integrating native shrubs into high country agricultural landscapes can support greater C sequestration and multiple co-benefits that include other soil (and water) quality improvements, improved trace element access for stock, and restored biodiversity and cultural values (Dickinson et al., 2015; Buckley et al., 2023). To scale these benefits, coordinated efforts between researchers, farmers, and policymakers are essential. A pathway is evident in these findings for the protection and regeneration of native vegetation in high country agricultural landscapes to help mitigate C emissions.

#### AUTHOR CONTRIBUTIONS

**Shyam Provost:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; visualization; writing—original draft; writing—review and editing. **Thomas M. R. Maxwell:** Conceptualization; methodology; supervision. **Niklas J. Lehto:** Conceptualization; formal analysis; methodology; supervision; writing—review and editing. **Nicholas Dickinson:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing—original draft; writing—review and editing.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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