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RESEARCH ARTICLE

Companion species mitigate nutrient constraints in high country grasslands in New Zealand

Zhang Wei · Thomas M. R. Maxwell · Brett Robinson · Nicholas Dickinson

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Abstract
Background Experimental work using pot trials and mesocosm studies has indicated that species combinations are more effective than single species mitigating the soil nutrient constraints that limit pasture productivity in New Zealand's hill country, but there is little field evidence to support this.
Aim We question whether coexistence of species provides an opportunity to facilitate enhanced uptake and improved procurement of key soil nutrients in these mid-altitude grasslands.
Methods Native and exotic legumes and co-occurring plant species were sampled according to whether they were growing together in close proximity or in single species patches. Foliar concentrations of nutrients were compared.
Results Nutrient concentrations in a native broom, *Carmichaelia petriei*, were higher when it was growing in combination with native tussock grasses. Higher concentrations of eight nutrients were recorded in foliage of an exotic legume, *Lotus pedunculatus*, when it was growing with native grasses or within the acuminate foliage of *Aciphylla aurea* (golden spaniard). Foliar concentrations of only P and Mn were elevated in white clover (*Trifolium repens*) foliage when it was growing in combination with grasses.
Conclusions These findings point to mutual facilitation of nutrient uptake by combinations of species growing together. Some species that are less desirable from an agricultural perspective improve acquisition of soil nutrients by the plant community. Novel native species assemblages represent a potential opportunity to refine pasture management, facilitating optimal exploitation of nutrients. This could reduce fertiliser requirements and enhance and protect native biodiversity in pastoral grasslands.

Keywords Mutualism · Biogeochemistry · Trace elements · Biodiversity · Pasture production

Introduction

Steep hill country at altitudes of about 400—1000 m accounts for 37% of New Zealand's land area, with approximately half of this being pastoral farmland (Thom 2016; Stats[NZ] 2021). Future environmental and economic resilience of this landscape is considered to be critical, although this is a multi-faceted and complex management issue (Brower et al. 2020; Rissman et al. 2021; Tozer et al. 2021). Our thesis

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Z. Wei · T. M. R. Maxwell · N. Dickinson (✉)
Faculty of Agriculture and Life Sciences, Lincoln University, Lincoln 7647, Christchurch, New Zealand
e-mail: Nicholas.Dickinson@lincoln.ac.nz

B. Robinson
Department of Chemistry, University of Canterbury, Christchurch 8140, New Zealand

is that sustainable agricultural development requires more knowledge of nutrient dynamics in the context of biodiversity in both pastoral and conservation grasslands.

Earlier forest clearance, historic overgrazing and associated soil erosion have provided scope for rebuilding hill country soils through improved pasture management. This has already been occurring for several decades through better land management, prevention of overgrazing and rabbit control (Parfitt et al. 2014; Schipper et al 2017). Potentially this could be enhanced further through restoration of native vegetation and incorporation of native species into existing naturalised exotic pasture (Trotter et al 2005). Native plant species are likely to be better adapted to the natural environment, but they are low yielding and of much lesser forage value. For this reason, agricultural management has focussed on conversion of native vegetation and replacement with more productive exotic species. However, pasture and stock production in the hill country are constrained by low soil pH and fertility, particularly in terms of phosphorus, sulphur and trace elements that include molybdenum and boron (Hendrie et al. 2021). These deficiencies restrict the successful establishment of clovers and other nitrogen (N) -fixing plants. Mt Grand Station, the location of the present study, provides a typical example of hill country conditions in these respects (Maxwell et al. 2010, 2016; Zhang et al. 2022a).

Top dressing with lime and fertilisers is largely impractical and too costly due to topography and the large area of land that will only support limited yields of herbage and stock in the prevailing climate and environment. During little more than 150 years since conversion of this landscape to sheep farming, oversowing with exotic species of grasses and legumes has substantially improved productivity (Bork et al. 2017). Hill country sheep and beef farming plays a highly important role in the nation's economy (Scrimgeour 2016; Stats^{NZ} 2021). Nevertheless, both establishment and sustainability of improved pasture with a suitable component of annual and perennial legumes remains a challenge; seasonal resilience is difficult to achieve and there is also encroachment by less desirable invasive and exotic species of grasses and shrubs.

A better understanding of the coexistence of native vegetation with introduced grasses and legumes in the hill country environment may be of benefit to both agriculture and conservation. We have previously reported the results of experimental work of plant uptake of nutrients from hill country soils to investigate the compatibility of both exotic and native plants with contrasting root systems. Pot trials provided evidence of functional compatibility of mixed-species rhizospheres that facilitate and improve the procurement of limiting soil nutrients (Zhang et al. 2022b). We identified the existence of a mutualistic relationship between legumes and grasses that provided nutritional benefits not just to grasses, but also to legumes (Zhang et al. 2022c). However, in that study, a native tussock grass had lower N when growing with the exotic legumes that may reflect a lack of adaptation to coexistence. More recently published mesocosm studies used soil cores with component vegetation assemblages that were extracted from unfertilised grassland in the hill country, and then transferred to a controlled environment growth chamber (Zhang et al. 2022a). Once again, species co-existence was beneficial in terms of uptake of key soil nutrient; facilitation from grasses to clovers was evident.

The aim of the research reported in the present paper was to investigate whether the same type of facilitation between species could be demonstrated in situ in a hill country grassland (Fig. 1). This sampling exercise was an attempt to validate earlier ex situ findings that legumes derive nutritional benefits from growing with grasses in terms of procurement of trace elements in limited supply in the hill country soils. Our hypothesis was simply that plants growing with companion species would have demonstrably different foliar concentrations of key nutrient elements compared to the same species growing alone.

Site and methods

This study was carried out at Mt Grand Station, a Lincoln University owned hill country pastoral farm situated in Hawea, Central Otago on South Island. The soils in the region have been created from the breakdown of schist, loess, and alluvial gravels (Molloy 1998; Duncan et al. 1997). The high country soils are light and prone to erosion by wind and water, especially after the loss of vegetation. Soils on Mt Grand are acidic and of low fertility (Table 1). Soil phosphorus (P) is essential grass-clover pastoral farming systems; its supply and availability is possibly

Fig. 1 Hill country grassland at Mt Grand Station in Hawea, South Island, New Zealand. *Aciphylla aurea* (Golden spaniard) in the centre foreground amongst *Chionochloa rigida* snow tussocks, *Festuca novae-zelandiae* tussocks within exotic pasture grass vegetation in the middle distance, and more heavily grazed pasture in the background

Table 1 Soil concentrations of deficient soil nutrients recorded in the experimental soil, with typical ranges for agricultural soils in New Zealand (full details in Zhang et al. 2022a)

Determinant	Unit of Measurement	Recorded Concentration	Typical Range in NZ Soils
pH	pH units	4.49–7.16	5.7—6.2
Olsen Phosphorus [1]	mg L^{-1}	**6.3**	20—30
Phosphorus[2]*	mg kg^{-1}	551	200—1,500
Potassium [3]	mg kg^{-1}	**113**	117—234
Boron [4]	mg L^{-1}	**0.2**	0.6—1.2
Molybdenum [2]*	mg kg^{-1}	**0.05**	0.5—10.0
Nickel [2]*	mg kg^{-1}	**4.6**	20—30

Analyses and units of measurement follow standard methodology from a commercial laboratory and also Lincoln University Analytical Services*. Analyses by the commercial laboratory are routinely carried out on defined volume rather than mass of soil. Analytical methods were: Olsen extraction [1] followed by Molybdenum Blue colorimetry; HNO_3 – $HClO_4$ microwave digestion followed by ICP-OES determination [2]; 1 M Neutral ammonium acetate extraction followed by ICP-OES determination [3]; Mehlich 3 Extraction followed by ICP-OES [4]

Significant deficiencies are emboldened

the most significant constraint due *to* its promotion of the growth of clovers. Boron, Mo and nickel (Ni) were deficient in our analyses, although Sulphur (S) and a range of other micronutrients (cobalt, Co; copper, Cu; iron, Fe; manganese, Mn; Mo; zinc, Zn) are frequently in short supply for pasture plants and grazing livestock in New Zealand grasslands (Crush et al. 2018). The Mt Grand landscape provides a complex mosaic of microenvironments associated with altitude, aspect and vegetation cover (Duncan et al. 2001). Mt Grand Station (1607 ha) is mainly steep hill country (from 400 – 1445 m asl.); 60% is above 1000 m in 8 blocks, with 94% of land considered suitable for grazing. Summer soil moisture deficits constrain pasture production (annual rainfall is 690–800 mm).

Methodology in this study simply involved sampling and analysing foliage of a range of exotic and native legumes at different altitudes. Sampling locations were semi-randomly selected between altitudes of 700 – 1,000 m asl. in a walkover of the site on a single day by one individual (ZW) where species could be found both growing in close proximity and also in single species patches 0.5 – 3.0 m apart. Our assumption was that both above- and below-ground interactions between species would be markedly less when they were growing further apart. Visually comparable environments and similar soil were important selection criteria, and the reason why paired comparisons were always recorded within 3 m of each other. Above-ground non-woody plant biomass was sampled of legumes growing either in single species patches or in combination with exotic pasture grasses, a native tussock grass or a native acuminate umbellifer (*Aciphylla aurea*), all of which were widely established across the sampling site.

Vegetation across the sampling site varied with altitude and aspect, consisting of mixed communities of native tussock grassland species with oversown pasture grasses and legumes (Fig. 2), with scattered assemblages of woody shrubs (mostly *Discaria toumatou*, *Kunzea robusta* and *Coprosma propinqua*) (*see* DOC 2006; Duncan et al. 2001). Some invasive weeds are also well established, notably *Hieracium* spp. in inter-tussock spaces at higher parts of the altitude range, and an invasive shrub *Rosa rubiginosa* in some lower parts. Tall pasture grasses are prominent at lower altitudes of this range, particularly *Anthoxanthum odoratum* (sweet vernal grass), *Agrostis capillaris* (browntop) and *Festuca rubra* (red fescue), with a scattered dispersion of *Trifolium* (clovers) and *Lotus* spp. Samples of the three pasture grasses were amalgamated. Tussock grassland and the proportion of native species in plant communities tends to increase with altitude, with patches of tall acuminate rosettes of *Aciphylla aurea* (golden spaniard). Native tussock grasses included *Chionochloa rigida* (narrow-leaved snow tussock), *Poa colensoi* (blue tussock) and *Festuca novae-zelandiae* (hard tussock). A native broom (*Carmichaelia petriei*), one of a small number of threatened native species of broom found across the station and in the high country (nzpcn.org.nz; DOC 2006; Mark 2012), was scattered mostly as individual plants across the sampling site. *Carmichaelia* spp. are commonly referred to as New Zealand brooms (Tan 2014). Their role in soil development in chronosequences through a large build-up of soil N and facilitating forest species has been reported previously (Bellingham et al. 2001).

Carmichaelia and the four groups of companion grasses (pasture grasses and three species of native tussock grasses) were sampled. Two exotic legumes, *Trifolium repens* (white clover) and *Lotus pedunculatus* (bird's-foot trefoil) and their companion native grass, *Festuca novae-zelandiae* (fescue tussock) and *Chionochloa rigida amara* (narrow-leaved snow tussock), were collected. *Lotus* was also sampled that was growing with or adjacent to *Aciphylla aurea*. Five replicates were sampled for each legume, each by excising five leaves across the canopy. Five replicates of each grass were sampled in the same way. All plant samples were collected at least 2 cm from the ground to avoid soil contamination of samples. All the plants were dried (48 h, 65 °C), finely ground in a mill, then microwave digested followed by elemental analysis using ICP-MS (7500cx, Agilent Technologies) using standard protocols. Total N was analysed using an Elementar Rapid Max N Elemental Analyser. Data that were not normally distributed were

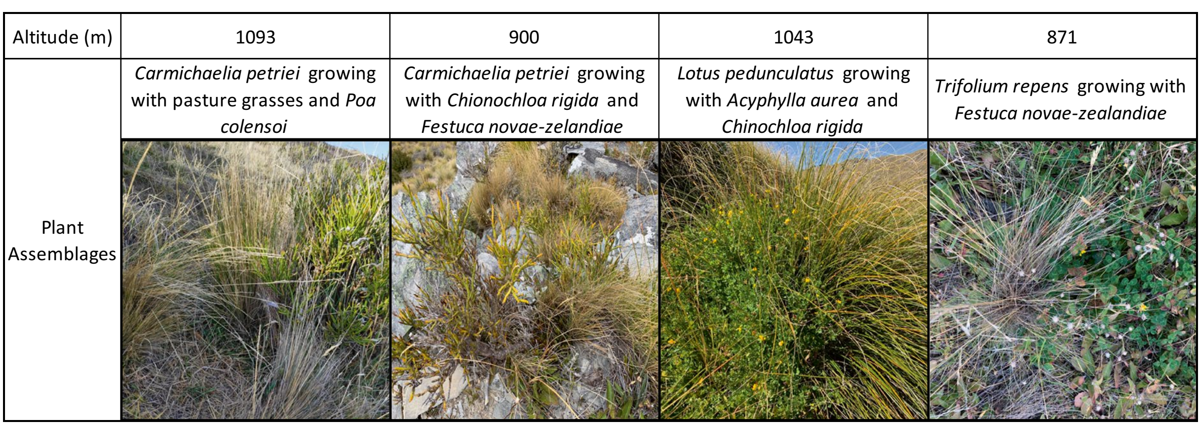

Fig. 2 Sampling locations at Mt Grand Station

log-transformed before analysis. Differences between means were determined using one-way ANOVA, with post-hoc Fisher LSD test. All analyses were conducted using Minitab 19.

Results

The native broom (*Carmichaelia petriei*) had significantly higher above-ground tissue concentrations of several elements when it was growing with companion species of grasses. Higher foliar concentrations of K, Ca, Mg and B were recorded when it was growing with pasture grasses and with *P. collensoi* at lower altitudes of the sampling range (Fig. 3A) and higher Mn, Zn and Ni when growing with *F. novae-zelandiae* at higher altitudes of the sampling range (Fig. 3B). Conversely, the two larger native tussock grasses tended to have lower foliar concentrations of nutrients when growing together with broom (Fig. 4). This was much less evident in the pasture grasses and the small blue tussock, *P. colensoi*. Of all chemical elements, only K and Mn were elevated in grasses growing with broom.

Foliar concentrations of eight nutrients in *Lotus* foliage were higher when it was growing with either *C. rigida* or *A. aurea*, or with both (Fig. 5); Fe was the only element in lower concentrations. Snow

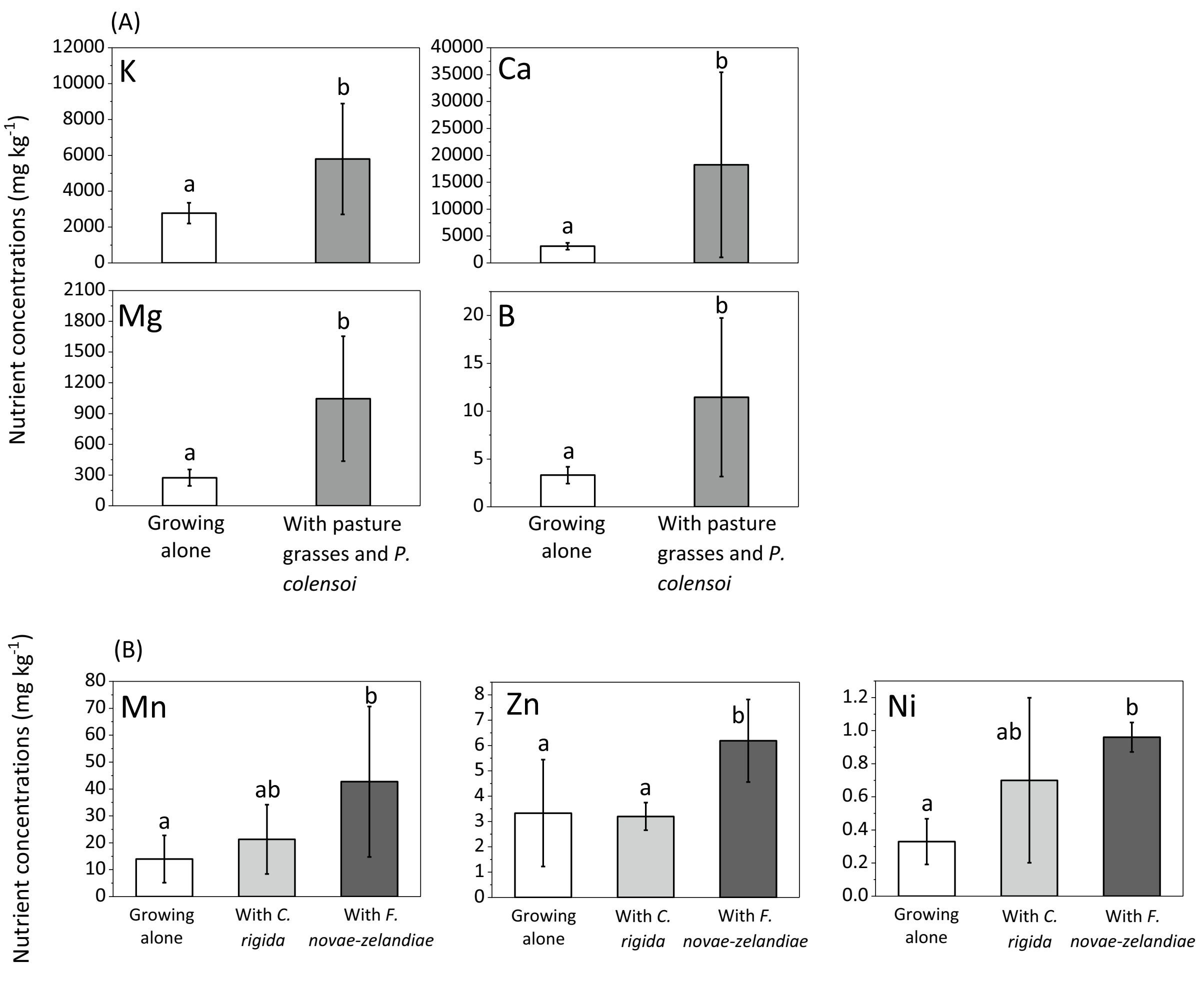

Fig. 3 Nutrient concentrations in green stems and foliage of broom (*Carmichaelia petriei*) and the four groups of grasses (pasture grasses, *Poa colensoi*, *Chionochloa rigida* and *Festuca novae-zelandiae*). Figure illustrates only elements when significate differences were recorded. Histogram bars are means ± standard deviations. Data were log transformed prior to analysis. Different letters separately indicate significant differences ($P < 0.05$)

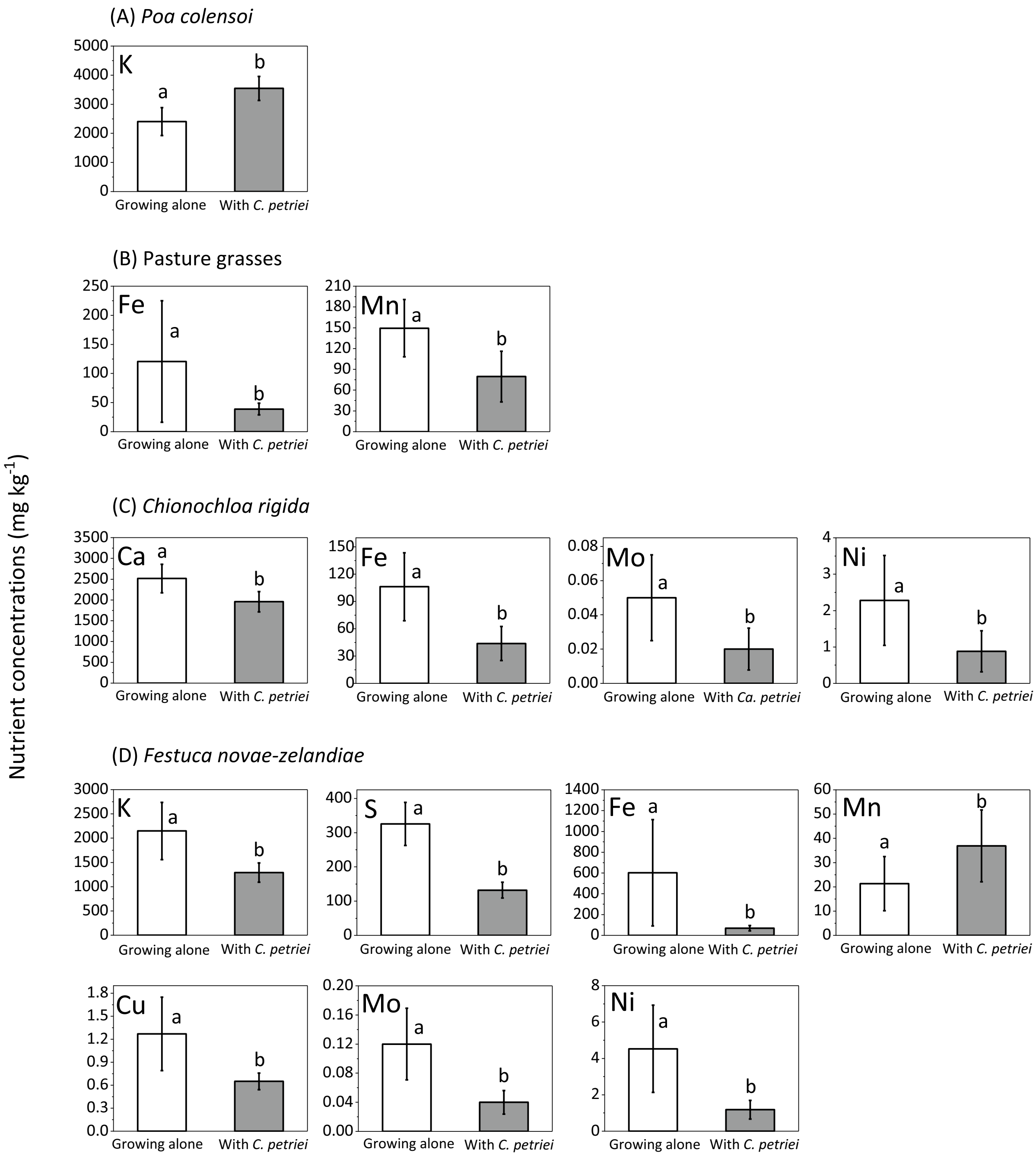

Fig. 4 Nutrient concentrations in foliage of the four groups of grasses, (**A**) *Poa colensoi*, (**B**) pasture grasses, (**C**) *Chionochloa rigida*, and (**D**) *Festuca novae zelandiae* according to whether they were growing alone or with a native broom (*Carmichaelia petriei*). Figure illustrates only elements when significate differences were recorded. Histogram bars are means ± standard deviations. Different letters separately indicate significant differences ($P < 0.05$)

tussock, *C. rigida*, foliage had significantly higher foliar concentrations of N, Zn, Cu and Mo when growing with *Lotus* (Fig. 6). In contrast, higher P and Mn concentrations in the foliage of *Trifolium* were in when it was growing with *Festuca novae-zelandiae* were the only significant differences recorded in

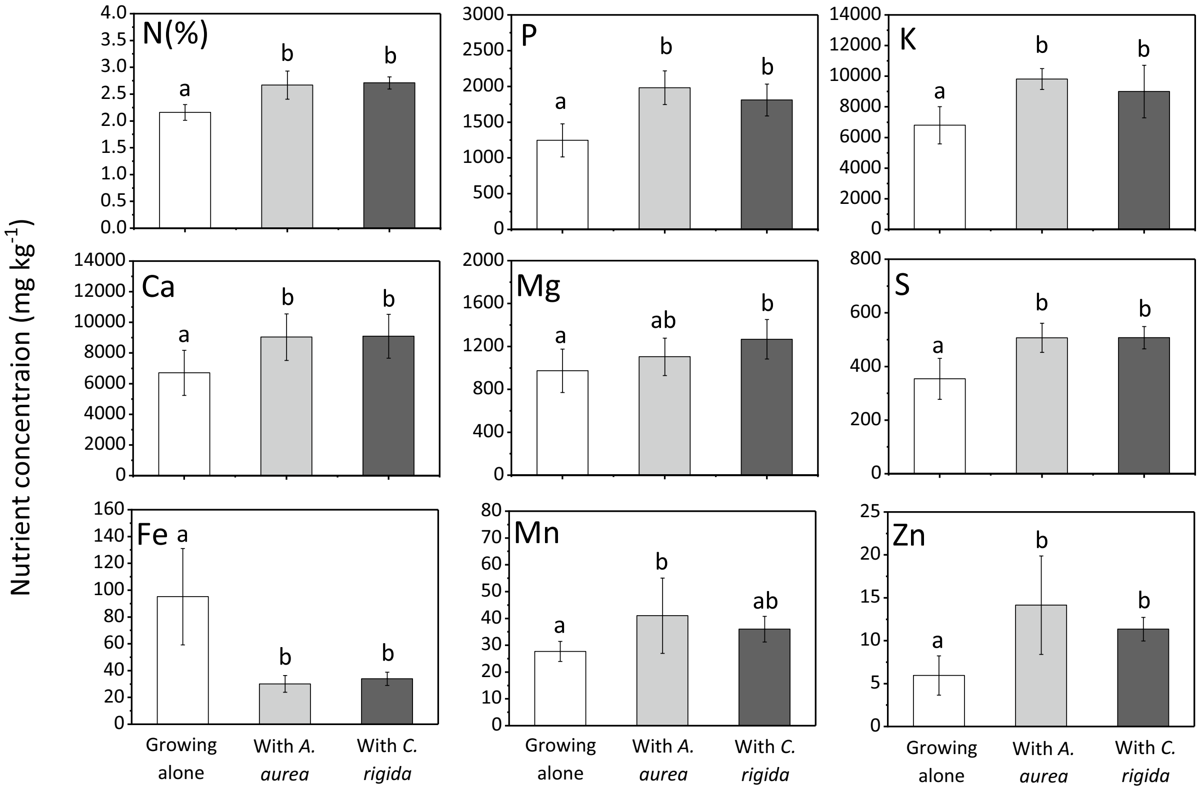

Fig. 5 Nutrient concentrations in foliage of *Lotus pedunculatus* according to whether it was growing alone or together with *Acyphylla aurea* or *Chionochloa rigida*. Figure illustrates only elements when significate differences were recorded. Histogram bars are means ± standard deviations. Different letters separately indicate significant differences ($P < 0.05$)

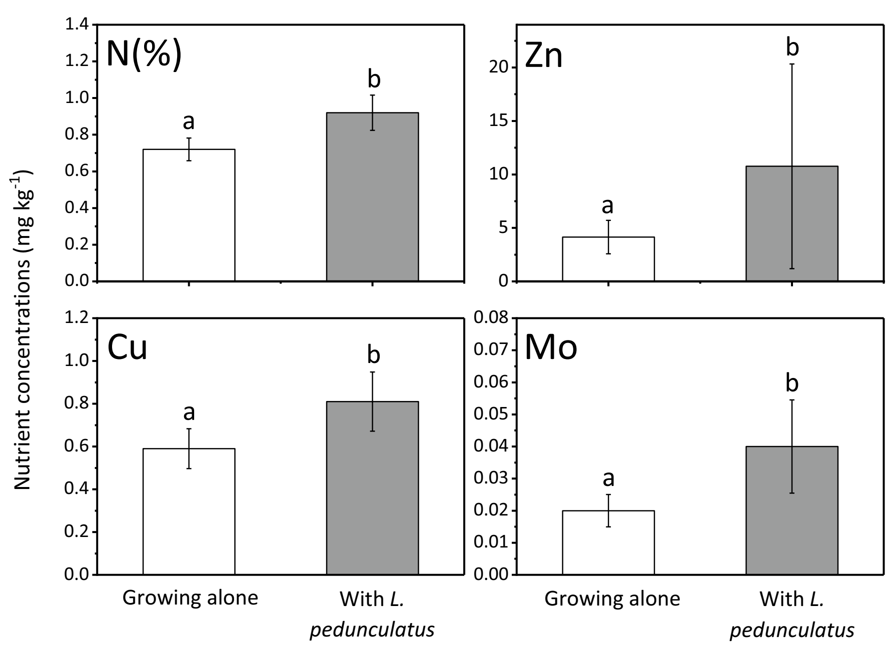

Fig. 6 Nutrient concentrations in foliage of *Chionochloa rigida* according to whether it was growing alone or together with *Lotus pedunculatus*. Figure illustrates only elements when significate differences were recorded. Histogram bars are means ± standard deviations. Different letters separately indicate significant differences ($P < 0.05$)

combinations of clover or grasses (Fig. 7). No data are available for foliar concentrations of nutrients in *A. aurea*.

Discussion

This study provides field validation that broadly supports the findings of earlier ex situ experimental work (Zhang et al 2022a, 2022c), supporting our hypothesis that plants growing with companion species would have demonstrably different foliar concentrations of key nutrient elements compared to the same species growing alone. These findings provide field evidence of significant benefits of grasses to legume nutrition, by facilitating the procurement of key nutrients. When growing with grasses, legume foliage frequently had higher concentrations of P, K, S and Mn. Improved uptake of six other elements (Ca, Mg, S, Zn, B, Ni) was recorded in more than a single study (Table 2). When growing with legumes, higher foliar concentrations of K, but lower Ca, Fe and Mn were recorded in grasses.

There are natural differences in foliar trace element concentrations between different species of legumes. For example, in pot experiments in which the growth of twelve species of legumes (including nine species of T*rifolium* and *Lotus pedunculatus*) were grown in South Island high country soil, comparable to the site of the present study, Jordan (2011) found a wide range of shoot concentration of P (0.11 – 0.26%), Mo (0.23 – 2.3 mg kg $^{-1}$) and B (6.4 – 17.7 mg kg $^{-1}$). Among the species, *T repens* and *L. pedunculatus* were near the upper part of the range for P, with concentration similar to those in the present study. Mo was much higher than the present study, but the soil had been limed in the earlier study which would have provided a supply of this element. Boron was at the lower part of the range in both these species. Foliar concentrations of nutrients in legumes are also likely to differ within the same species, largely dependent on the type of soil and its fertility (Nguyen et al. 2020). Gounden et al. (2018) collected several species of *Trifolium* from different localities, and recorded large differences in Fe, Ca, and Mn. The process of symbiotic N fixation (Liu et al. 2018), requires the interplay of several variables involving rhizobial communities (Tan et al. 2015). These include the specificity and extent of rhizobial infection (Andrews and Andrews 2017), root nodule development (Schwember et al. 2019) and other factors such as mycorrhizal associations (Sprent and James 2007), all interacting with multiple nutrient availability in soil and uptake by legumes and grasses (e.g. Becana et al. 2018).

Undoubtedly, at the site of the present study there would be significant spatial variability in a range of soil nutrients associated with soil development, altitude, slope, aspect, erosion, vegetation cover and stock activity. However, this would be unlikely to explain differences in above-ground concentrations of nutrients recorded between legumes and grasses. Every species that was sampled when growing singly or in combination was within 3 m of each other. Furthermore, all replicates for each species pair were collected within a maximum land area of approximately 100 m ^{2}. The sampling procedure involved identifying

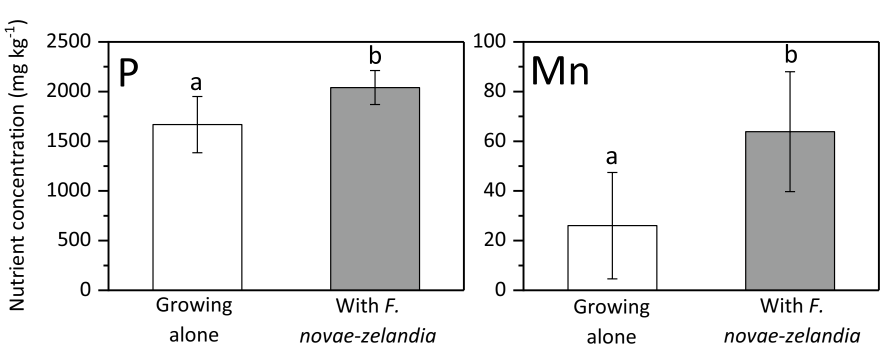

Fig. 7 Nutrient concentrations in foliage of *Trifolium repens* (white clover) when it was growing alone or with *Festuca novae-zelandiae*. Figure illustrates only elements when significate differences were recorded. Histogram bars are means ± standard deviations. Different letters separately indicate significant differences ($P < 0.05$)

Table 2 Comparison of the results with two earlier studies. The increase (+, dark shading), no significant change (light shading) or decrease (-, no shading) of foliar nutrient concentration in (A) legume spp. when growing with companion grasses, and (B) grass spp. when growing with companion legumes.

(A) Legumes

	Zhang et al, 2022c			Zhang et al, 2022a	Present findings		
Experiment type	Pot experiment		Field sample (Fertile paddock)	*Ex-situ* Soil core	Field sample		
Species / Nutrients	*Trifolium repens*	*Lotus pedunculatus*	*Trifolium repens*	*Trifolium repens*	*Trifolium repens*	*Lotus pedunculatus*	*Carmichaelia petriei*
Phosphorus	+	+	-	+	+	+	
Potassium		+	+	+		+	+
Calcium		-	+			+	+
Magnesium		-				+	+
Sulphur		+		+		+	
Iron						-	
Manganese	-	-	+		+	+	+
Zinc						+	+
Copper		-	+				
Boron		-	+				+
Molybdenum		-	-				
Nickel		-		+			+

(B) Grasses

	Zhang et al, 2022 c			Zhang et al, 2022 a	Present findings			
Experiment type	Pot			Soil core	Field sample			
Species / Nutrients	*Lolium perenne*	*Dactylis glomerata*	*Festuca novae-zelandiae*	Native grasses and Herbs	Pasture grasses	*Poa colensoi*	*Chionochloa rigida*	*Festuca novae-zelandiae*
Phosphorus	-		-					
Potassium	+	-	-	-		+		-
Calcium			-	-			-	
Magnesium	-			-				
Sulphur	+							-
Iron					-		-	-
Manganese				-	-			+
Zinc		+	-					
Copper	-			+				-
Boron	-		-	-				
Molybdenum	-						-	-
Nickel		+		+			-	-

locations containing each species combination, then immediately sampling adjacent patches where each species was growing alone, providing direct comparisons between plants growing alone and with companion species. It is unlikely the measured differences could be accounted for by spatial variability, although this probably explains the high variability of data about the means. Nutrients can be patchy (e.g. Emeterio et al., 2021) and soils are impacted by random historic occurrences that include organic input from animals. However, in the present study, the important characteristic they have in common is deficiencies of the same range of nutrients. The significance of the recorded differences between plants growing alone and with companion species is associated with the replicated paired comparisons.

Plant growth is influenced by multiple stressors; for example drought rather than soil nutrients would be the main limitation to plant growth during summer. Intraspecific competition in monospecific patches is likely to also play a significant role affecting nutrient uptake. Another consideration in this study is whether preferential grazing influenced the recorded differences between plants growing alone and those with companion species. The high country farm is fenced into large grazing blocks, each typically 100 + ha in size; the blocks that were sampled are all extensively grazed by sheep but also visited by several wild mammalian pests including rabbits and deer. Studies of compensatory growth in response to grazing (the compensatory continuum hypothesis) have provided some evidence that soil nutrient availability may affect compensatory growth by grazed plants (Wise and Abrahamson 2005; Venter et al. 2021). In studies of rotational grazing of fertile farmed grasslands, it is known that sustained defoliation of vegetation beyond its capacity to regrow subsequently degrades productivity. In the present study, preferential grazing of the legumes would undoubtedly deplete the available nutrient pool for the grasses, but the legume would then have more requirement for trace elements from the grasses. This certainly could be the start of the mechanistic explanation.

Native plants that fix N are largely lacking in New Zealand's grassland flora; brooms are one of only a few exceptions, together with a small number of woody shrubs (e.g. *Discaria toumatou*, Rhamnaceae and *Sophora* spp., Fabaceae). The amount of N cycled was much less before vigorous N-fixing plants were introduced (Wardle 1991). In low fertility soils, it is well established that legume-grass assemblages are more productive than grassland without N-fixing plants (e.g. Berenji et al. 2017). Legumes have a higher demand than grasses for P, S and other trace elements essential for N_2 fixation (Caradus 1980; Yuvaraj et al. 2020). However, many grass species have been shown to activate fixed phosphorus in the soil by releasing organic acid root exudates (Li et al. 2003, 2014). This obviously provides scope for neighbouring N-fixing plants and grasses to exchange mobilised soil nutrients. Unravelling the likely explanations for changes in patterns of nutrient uptake was discussed in an earlier paper (Zhang et al. 2022c).

The present study showed benefits to *Carmichaelia* in terms of acquisition of a range of nutrients, corresponding with declining concentration of several elements in companion grasses that support the hypothesis of this study. The genus *Carmichaelia* contains about 30 species, all but one from New Zealand, although only a handful of species extend into the high country (Mark 2012). Rhizobial symbionts have been described for some species (Tan 2014; Tan et al. 2013) and there is evidence from chronosequences that native brooms provide N benefits to coexisting plant species and in soil and ecosystem development in (Bellingham et al. 2001; Lagerstrom et al. 2011). There is, however, far more research on an exotic *Cytisus scoparius* (Scotch broom), which is highly invasive and widespread in New Zealand, including montane shrubland and tussock grasslands (Bellingham and Coomes 2003), and of which more is known of its effect on soil N (Drake 2011; Broadbent et al. 2017). Little attention has been given to modification of soil biogeochemistry by native species. Legumes including brooms provide better nutrition than grasses by stock, but they are also preferentially grazed, suggesting this a possible example of how a threatened endemic species could provide a valuable component of pastoral grassland in the high country, even though grazing potentially threatens their resilience and conservation.

Lotus pedunculatus also received nutritional benefits from companion grasses. A marked effect of higher foliar nutrient concentrations of eight nutrient elements including N by *Lotus* when growing with its two companion species was evident. This legume develops a dense superficial underground system of roots and rhizomes, although above-ground recovery from defoliation is slow and it thrives only under light grazing pressure (Espie 1987). Old rhizomes breakdown in winter and spring but later propagate new discrete plants. This species thrives better than *Trifolium repens* on acid soils with low P (Stewart and Charlton 2006), but is generally considered to have a lesser effect than clovers on the growth of companion grasses (Nordmeyer and Davis 1977). The findings of the present study suggests that *Lotus* may provide a good example of a relationship between exotic legume and a native grass that is beneficial for grazing and stock production, and also to conservation of native species. Foliar concentrations of N and three key trace elements (Zn, Cu and Mo) were enhanced in snow tussocks at higher parts of the altitude range when growing together with *Lotus*.

The present study did not provide similar evidence to show that *Trifolium repens* benefited from associations with any of the grasses, apart from improved concentrations of P and Mn when growing with *Festuca novae-zelandiae*. Supply of P is critical to P fixation (Liu et al. 2018). Manganese improves drought tolerance in legumes, being required for degradation of ureide, an acyl derivative of urea, which otherwise inhibits N fixation (Purcell et al. 2000). *F. novae-zelandiae* was the most widespread native grass in lower altitudes of the sampling area and is typical of dry and windy locations in South Island. An early study found that *Poa colensoi* has VA mycorrhizal association, but the other two tussocks do not (Crush 1973). The relationship between different species of grasses requires further field investigation to support the finding of earlier pot experiments (Zhang et al. 2022b, 2022c). In view of the long history of attempts to establish different species of annual and perennial clovers in the New Zealand hill county, this requires more research.

In the two earlier ex situ studies (Zhang et al. 2022a, 2022c), elevated concentrations of nutrients in legumes often corresponded with lower concentrations of the same nutrients in grasses but, in the present study, there appeared to be less evidence this was the case. Without vegetation yield data from the sampling locations it is not possible to estimate the total mass of each nutrient extracted from the soil. However, mass balance calculations in the earlier studies showed that combinations of species enhanced overall exploitation of nutrients from defined volumes of soil, providing evidence of transgressive overyielding (Zhang et al. 2022a, 2022c). Undoubtedly, differences between studies can be attributed to differences between species in terms of requirements and rhizosphere biogeochemistry. Further study is required of the most significant species combinations that potentially could be managed to improve pasture productivity and to allow native species to be restored and sustained within this agricultural matrix.

Conclusion

The findings of the present work have shown that facilitation between species plays a role in nutrient procurement from soil in New Zealand's hill country grasslands. This points to a requirement for more detailed studies into the combined influence of mixed plant species on multiple nutrient availability in soil, and for better mechanistic explanations. There are synergies between legumes, grasses and other co-existing plant species that optimise acquisition of deficient chemical elements from soil. This extends to a range of nutrients in addition to N. Clearly, there is variability between species and species combinations, but we have provided evidence of improved uptake of P, K, S and Mn, also extending to six other elements.

Earlier reported work on facilitation of nutrient uptake between plant species has largely focussed on agricultural intercropping systems (e.g. Li et al. 2014) making similar linkage between P acquisition with phytosiderophores and Fe, Zn and Mn. Mechanistic explanations for facilitation are also well known in Western Australia flora (Lambers 2014). The present study provides similar insights into low fertility high country grasslands in New Zealand. These grasslands originated from oversown, invasive and naturalised exotic species that have become established and maintained within large expanses of native vegetation, for the purpose of providing more productive fodder for stock. The novelty of the present findings is to introduce the concept of facilitation into these novel native ecosystems. These grasslands have high economic value for agriculture, but also exceptional conservation value as they contain the largest proportion of the endemic species of New Zealand.

Novel native plant community assemblages in this agroecological mosaic represent a potential opportunity to refine pasture management by exploiting combinations of plant species that facilitate optimal exploitation of nutrients, with less reliance on fertilisers. Furthermore, informing ecological knowledge of the role of nutrient acquisition in the origin and maintenance of biodiversity in grassland is an additional outcome of this research. Incorporating more native species into this mid-altitude pastoral landscape would provide undoubted benefits to protection of biodiversity through land sharing. Generally, however, native plants have little resilience to or protection against ruminants, whether or not they are preferentially grazed. Prior to relatively recent human arrival in New Zealand, the endemic flora evolved and existed largely without fertile soils and in the absence of mammals. Native brooms provide one of only a small number of legumes that provide an obvious nutrition contribution to grazers through fixing N. Otherwise, native species persist in contemporary pastoral grassland occasionally through their physical defences, as in golden spaniard, or though being a secondary choice for grazing, as in snow tussocks. Nonetheless, grasses and other species that are less desirable from an agricultural perspective clearly play a facilitation role in nutrient procurement by species that are more desirable for agriculture or conservation. Combinations of plants enhance the acquisition of key soil nutrients. These findings justify more attention to enhancement rather than restriction of plant species diversity in the vegetation matrix of the New Zealand hill country.

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Authors' contribution All authors contributed to the planning and execution of the project, and to manuscript preparation. Zhang Wei carried out the practical work and data analysis as part of his PhD programme supervised by Nicholas Dickinson, Thomas Maxwell and Brett Robinson. Nicholas Dickinson is responsible for the final manuscript draft.

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Data availability Lincoln University Data Repository.

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Declarations

Conflict of interest There are no conflicts of interest.

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