plants

MDPI

Article

Plant Species Complementarity in Low-Fertility Degraded Soil

Zhang Wei [1], Thomas Maxwell [1], Brett Robinson [2] and Nicholas Dickinson [1,*]

[1] Faculty of Agriculture and Life Sciences, Lincoln University, Lincoln, Christchurch 7647, New Zealand; wei.zhang@lincolnuni.ac.nz (Z.W.); tom.maxwell@lincoln.ac.nz (T.M.)
[2] Department of Chemistry, University of Canterbury, Christchurch 8140, New Zealand; brett.robinson@canterbury.ac.nz
* Correspondence: nicholas.dickinson@lincoln.ac.nz; Tel.: +64-3-423-0741

Abstract: The aim of this study was to investigate the compatibility of plants with contrasting root systems, in terms of procurement of limiting soil nutrients. Paired combinations of species of proteas and grasses were grown in a pot experiment using soil from a site with impoverished vegetation and degraded soil. The soil contained sufficient N but was low to deficient in P, Mn, S, Fe, and B. The uptake of chemical elements into the foliage differed significantly according to whether the plants were growing as single or mixed species. When two species of *Grevillea* and grasses with evolutionary origins in low fertility soils were growing together, there was an enhanced uptake of P and Mn, in one or both species, in addition to other elements that were in low concentrations in the experimental soil. In contrast to this, *Protea neriifolia* that probably originated from a more fertile soil procured lesser amounts of the six elements from the soil when growing together with grasses. Two grasses tolerant of less fertile soils (*Dactylis glomerata* and *Poa cita*) obtained more nutrients when they grew together with proteas; this was a much stronger neighbour effect than was measured in *Lolium perenne* which is better adapted to high fertility soils. The findings illustrate both the functional compatibility and competition for plant nutrients in mixed-species rhizospheres. Species combinations substantially increased the acquisition of key elements from the soil nutrient pool.

Keywords: soil nutrients; plant nutrition; co-existence; rhizosphere; phosphorus; manganese

check for updates

Citation: Wei, Z.; Maxwell, T.; Robinson, B.; Dickinson, N. Plant Species Complementarity in Low-Fertility Degraded Soil. *Plants* **2022**, *11*, 1370. https://doi.org/10.3390/plants11101370

Academic Editor: Sergey Loiko

Received: 30 March 2022
Accepted: 19 May 2022
Published: 21 May 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

There is great variability in the mobility of chemical elements in the rhizospheres of different species that is reflected in the exploitation of the soil nutrient pool and the uptake of nutrients by plants [1,2]. This would suggest that combinations of plant species may be more effective than single species at modifying the mobility and management of chemical elements in soils [3]. The hypothesis underlying this study is that plants naturally adapted to low fertility or degraded soils are likely to benefit by growing in combination with other species that possess different functional traits in the rhizosphere, since most plant species have similar fundamental metabolic demands for the same range of key nutrients [4]. A strategy of sharing different capabilities to procure key soil nutrients might prevail over the competition for access to a limited resource. Contrary to this, plants adapted to more fertile soils may be more likely to employ a competitive strategy to rapidly acquire a majority share of nutrients from a more plentiful pool of available soil nutrients. We test this hypothesis by growing a combination of plants that do not naturally occur together, but that are known to have different root functional traits that are adapted to either fertile or infertile soils, combinations readily found both in the Poaceae (grasses) and Proteaceae (all species are referred to using the generic term 'protea' in the present paper).

There are often added benefits to plant productivity from two or more plant species growing together. Intercropping in agriculture and horticulture provides increased yields, often referred to as transgressive overyielding [5–9], for example when legumes are grown together with other crops [10,11]. In this example, the fortuitous spillover of N fixed

by rhizobial symbionts from the legume to neighbouring plants is generally viewed as incidental, even though it seems unlikely that evolution has favoured an adaptation in plants that expends metabolic energy and resources towards obtaining N that is then readily shared with competitors. Recently, we have shown that grasses reciprocate in this relationship by procuring key trace elements in the rhizosphere that are then passed on to legumes [3]; grass—clover assemblages enhanced overall productivity and uptake of P, K, S, Mn, Cu, Mo, and B. The present paper investigates whether the sharing of phosphorus and key trace elements can also be identified between proteas and grasses of different origins when they grow together in soil with sufficient N for healthy growth, but with deficiencies of other key nutrients. We selected plant species that are known to possess contrasting root functional traits, and which did not share a common biogeographical origin.

The uptake of chemical elements is known to differ between species and according to whether plants are grown in monoculture or in mixed species assemblages [12], or naturally found in the same location and habitat [3]. However, investigations of the physiological traits associated with uptake seldom extend to a consideration of the two-way sharing of soil nutrients. One of the few more detailed examples of complementarity is with plants that produce cluster roots, found within a few plant families, including the Proteaceae and in a few crops such as *Lupinus albus* (white lupin) [13,14]. Cluster roots primarily enable plants to exploit less labile pools of soil phosphorus (P) in P-deficient soils, by releasing organic acids to mobilise mineral P that is bound to metal cations and organic complexes in the soil [15]. There is some evidence that cluster roots can also facilitate the acquisition of nutrients by neighbouring plants [16]. Different and contrasting strategies to acquire soil nutrients are employed by grasses, for example through different root structures [17], using mycorrhizal associations [18], or by secreting organic acids (phytosiderophores) [19]. Our assumption was that the acquisition of P, which is most often the predominant element limiting plant growth, would play a definitive role in our findings. Complementarity has previously been found to explain coexistence between different functional groups of grasses [20].

The aim of this study was to investigate species complementarity in the context of P and key trace elements, by measuring the uptake of nutrients into the foliage of species of different origins growing together artificially in nutrient-depleted soil. The work is particularly relevant to the management of species diversity in low-fertility production systems, but also has potential significance for phytoremediation science and practice, where exotic species are introduced to contaminated and degraded soils to manipulate chemical elements [21–23].

2. Results

Elevated concentrations of P and Mn were particularly notable in the *Grevillea* spp. when grown with grasses (Figure 1), in contrast to *Protea neriifolia* foliage which had lower Mn concentrations when it was grown with the grasses. On at least one of the two sampling occasions, *Grevillea barklyana* had higher foliar concentrations of most chemical elements when growing together with grasses, particularly with *Dactylis glomerata* (cocksfoot) (Figure 2; Appendix A, Table A1). Only three elements in G. Robin Hood foliage differed significantly when it was growing with grasses (Figure 2; Appendix A, Table A1). Five of the elements with higher concentrations (P, Mg, S, Mn, Zn, and B) were nutrients known to be deficient in the soil, but also included K and Mo. In contrast, lower concentrations of 5 elements in addition to P, were often recorded in *P. neriifolia* foliage when it had grown with grasses (Figure 3; Appendix A, Table A1).

There were fewer changes in the elemental concentrations of the two pasture grasses, *Dactylis glomerata* (cocksfoot) and *Lolium perenne* (perennial ryegrass), when they were growing with proteas, and this was mainly related to higher concentrations of P, K, and Ca (Figure 4). *Poa cita* (a tussock grass) was different, with significantly elevated foliar P, K, Ca, S, Mn, and Zn when it was growing with proteas (Appendix A, Table A2). Focusing on *D. glomerata*, as the grass with the most evident neighbour effects (Figure 5), there was a shift

in foliar nutrient concentrations of both proteas and grasses when they were growing with a neighbouring species, with a difference in nutrient uptake.

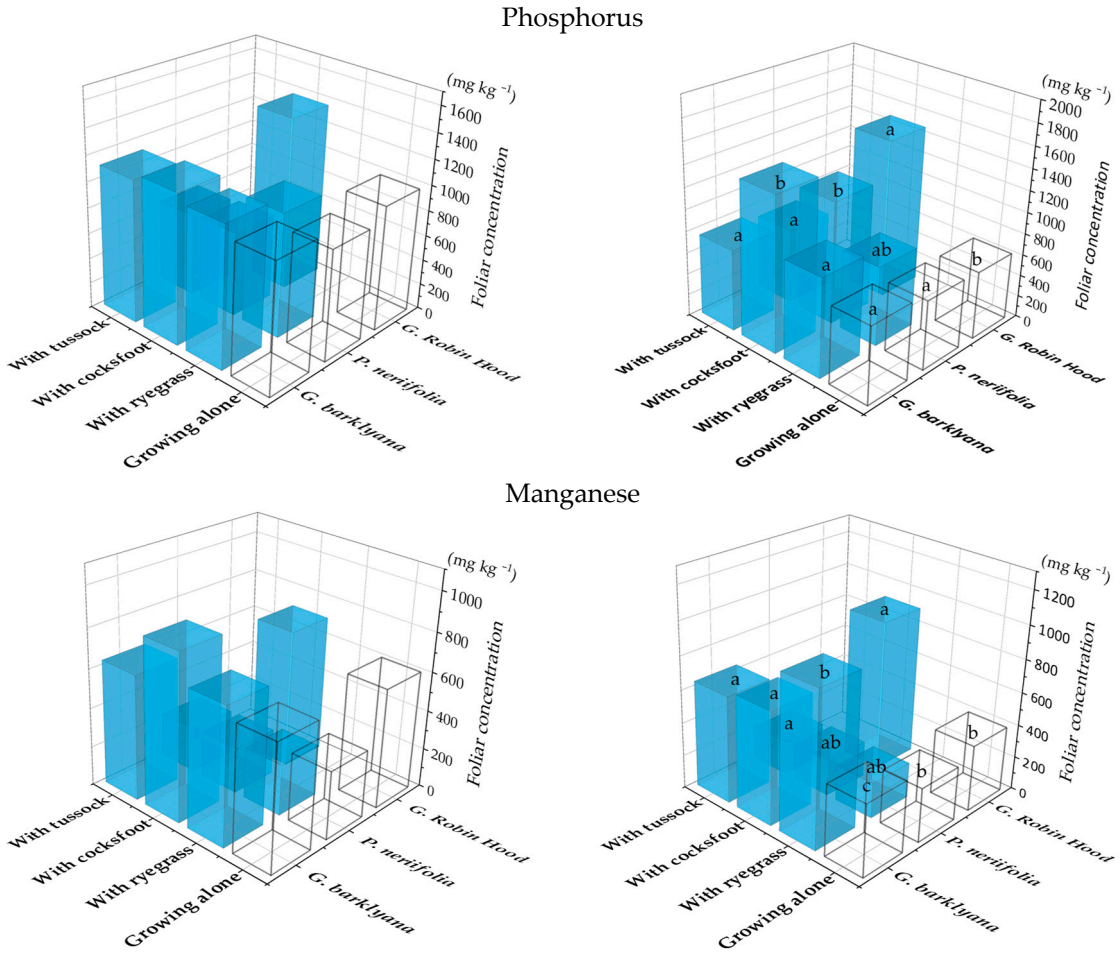

Figure 1. Phosphorus and manganese concentrations in the foliage of the three species of proteas when they were growing alone (open bars) or with one of three species of grass: *Lolium perenne* (ryegrass), *Dactylis glomerata* (cocksfoot), or *Poa cita* (tussock grass) (coloured bars). Charts show results of 1st (LHS) and 2nd (RHS) sampling. Different letters each indicate significant differences ($p < 0.05$) for each protea (full results in Appendix A, Table A1).

In terms of plant productivity, there were few significant differences in the biomass of the proteas or the grasses after they had grown with neighbouring plants, but the variability was high within each treatment (Figure 6). The exploitation of the soil pool of chemical elements may be more accurately represented by mass balance calculations (multiplication of dry wt. of foliage × nutrient concentration). This calculation was performed using data separately for each species (Figure 7; Appendix A, Table A3). More P, Mn, and Zn was procured by the *Grevillea* spp. but less by *P. neriifolia* when these species had grown in the same pots as the grasses. In percentage terms, neighbouring grasses only marginally reduced the biomass of protea foliage, but higher foliage concentrations of elements led to significantly increased total offtake of nutrients by as much as 100% in the proteas (Figure 8). There was a much lower biomass of grass foliage than of protea foliage, on average amounting to 11% of the latter, which meant that the total amount of each element extracted from the soil with the grasses was much less than the amount extracted by proteas (Appendix A, Table A3). Nonetheless, these calculations illustrated clear differences between *P. neriifolia* and the *Grevillea* spp., and between the different grass species (Figure 8). When the proteas and grasses were growing in combination with

each other, compared to growing as monocultures, they extracted substantially increased amounts of nutrients from the soil.

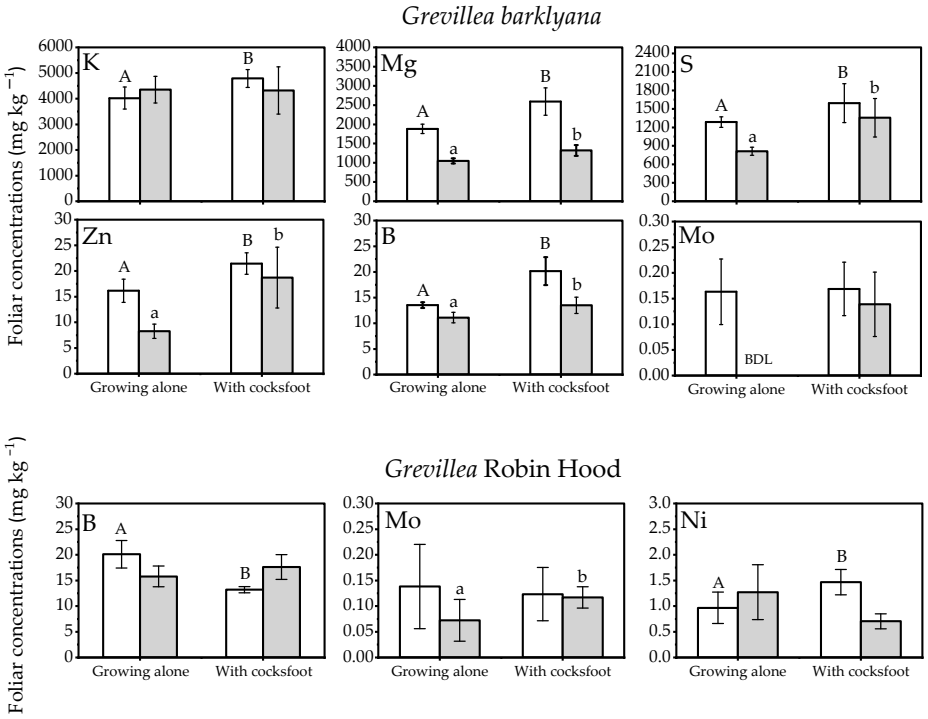

Figure 2. Nutrient concentrations in the foliage of the two *Grevillea* spp. when they were growing alone or together with *Dactylis glomerata* (cocksfoot) (open bars, first sampling; shaded bars, final sampling). Different letters each indicate significant differences ($p < 0.05$) within each sampling event (upper case letter indicate differences at the first sampling, lower case letters indicate significant differences at final sampling). Elements without significant differences are not shown (full results in Appendix A, Table A1).

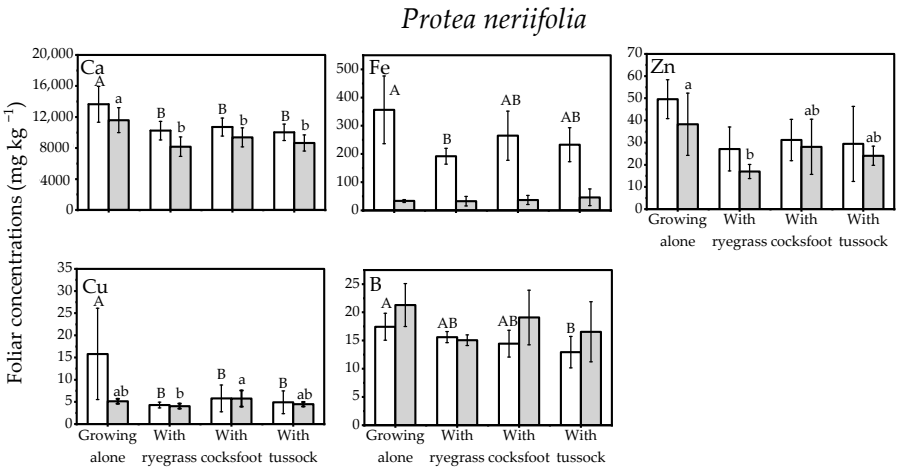

Figure 3. Nutrient concentrations in the foliage of the *Protea neriifolia* when grown alone or together with the three species of grass: *Lolium perenne* (ryegrass), *Dactylis glomerata* (cocksfoot), or *Poa cita* (tussock grass) (Open bars, first sampling; Shaded bars, final sampling). Different letters each indicate significant differences ($p < 0.05$) within each sampling event (upper case letters indicate differences at the first sampling, lower case letters indicate significant differences at final sampling). Elements without significant differences are not shown (full results in Appendix A, Table A1).

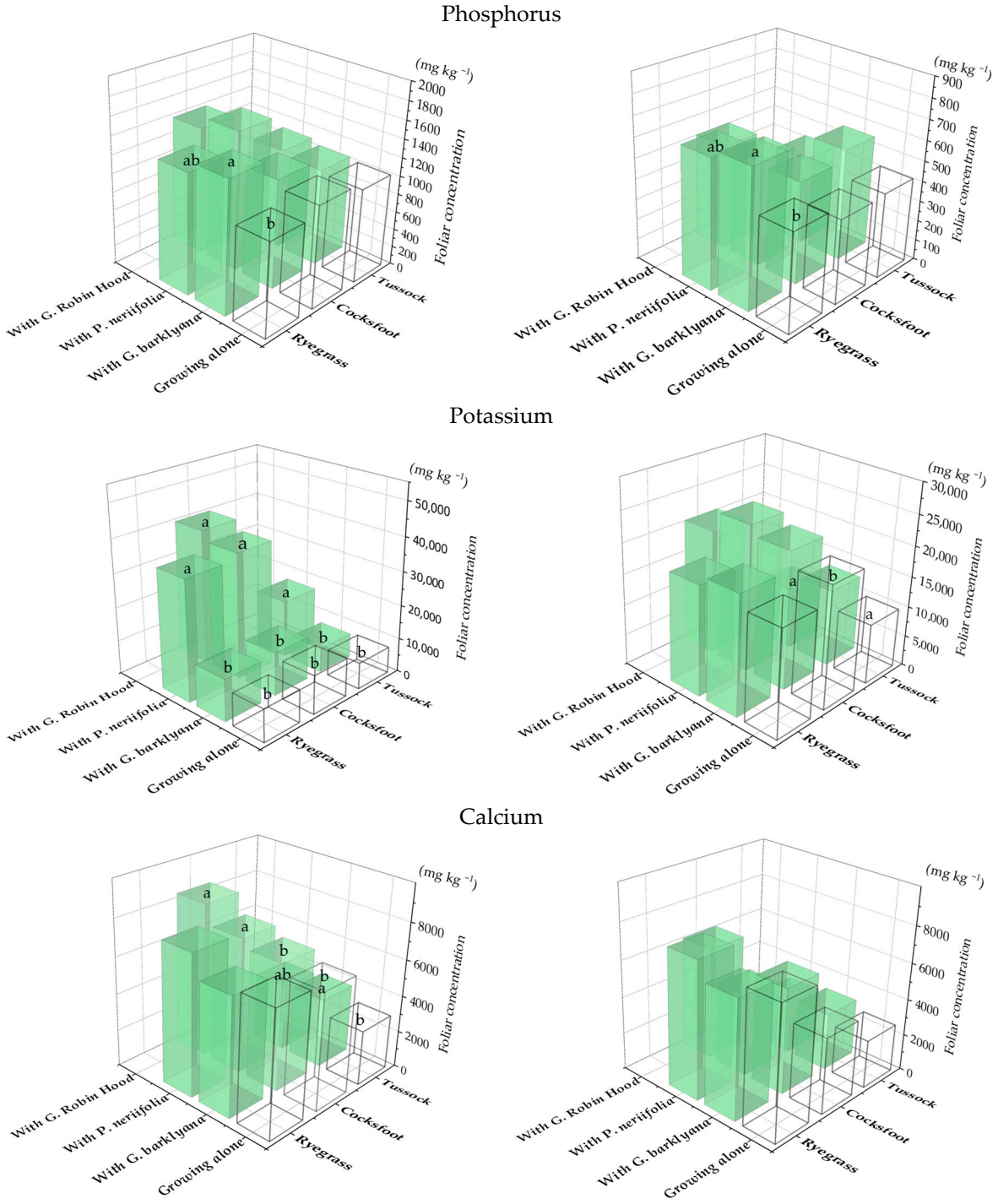

Figure 4. Phosphorus, Ca, and Mn concentrations in the foliage of the three species of grass (*Lolium perenne*, ryegrass; *Dactylis glomerata*, cocksfoot; *Poa cita*, tussock grass) when they were growing alone (open bars) or with one of three species of proteas (coloured bars). Charts show 1st (LHS) and 2nd (RHS) sampling. Different letters each indicate significant differences ($p < 0.05$) each for each species of grass (full data in Appendix A, Table A2).

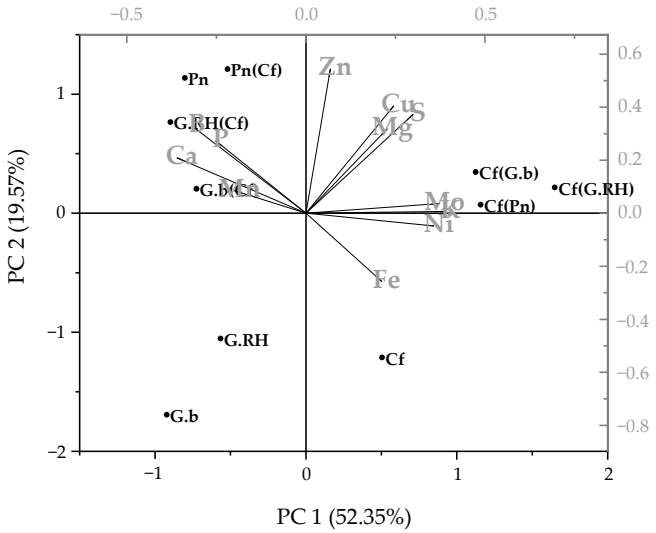

Figure 5. Principal Components Analysis describing foliar nutrient concentration data for each of the protea species (Gb, *Grevillea barklyana*; *Protea neriifolia*, Pn; Grevillea Robin Hood, G.RH) growing alone or with *Dactylis glomerata* (cocksfoot, Cf), and for cocksfoot growing alone or with each of the proteas. Abbreviations in brackets indicate the companion species.

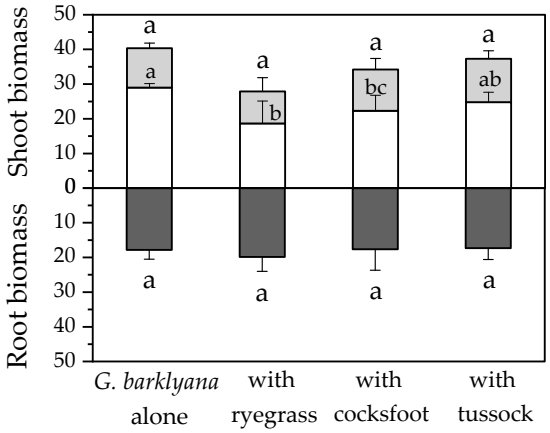

Figure 6. Harvested biomass of *Grevillea barklyana* (dry wt., g pot^{-1}) when it was grown alone or with one of the three species of grass: *Lolium perenne* (ryegrass), *Dactylis glomerata* (cocksfoot), or *Poa cita* (tussock grass). Shoot biomass shows stems (open bars) and foliage (shaded bars). Different letters indicate significant differences ($p < 0.05$) within separate plant components.

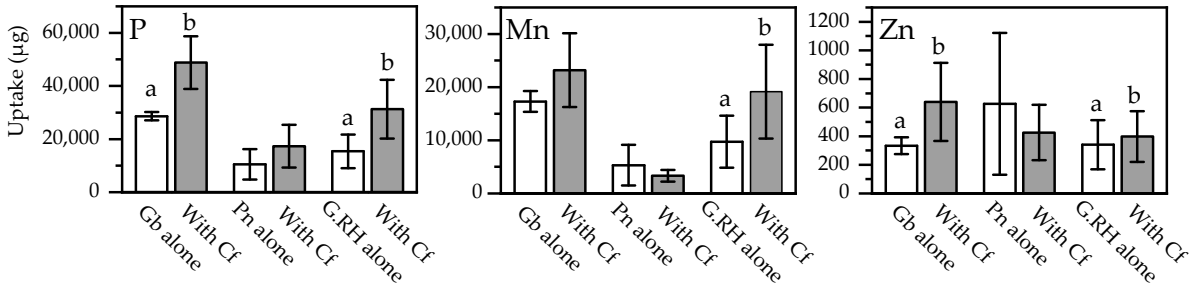

Figure 7. Total uptake of P, Mn, and Zn into foliage of each of the three species of Protea, when they were growing alone or with *Dactylis glomerata* (cocksfoot): Gb: *Grevillea barklyana*, Pn: *Protea neriifolia*, G.RH: Grevillea Robin Hood, Cf: Cocksfoot. Open bars, first sampling; shaded bars, final sampling. Different letters each indicate significant differences ($p < 0.05$) within each of the sampling events. Elements without significant differences are not shown (full data in Appendix A, Table A3).

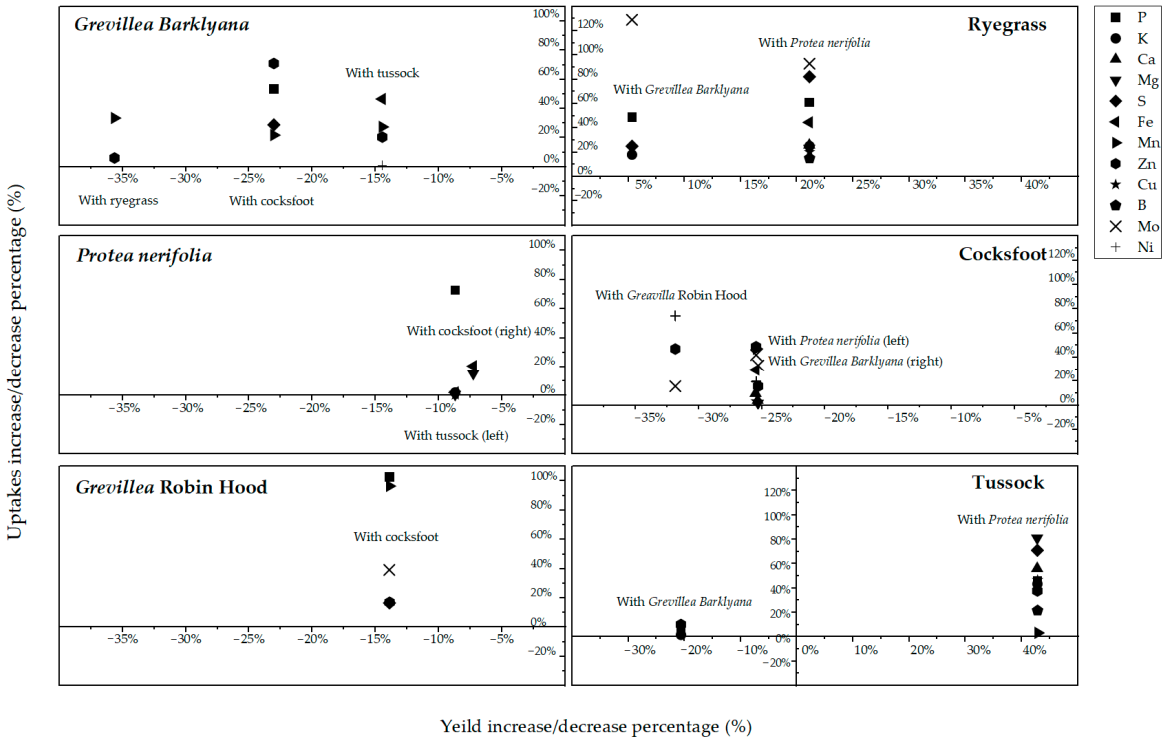

Figure 8. The percentage change in yield (horizontal axes) and total foliar uptake of key nutrients (vertical axes), when each of the protea and grass species (*Lolium perenne*, ryegrass; *Dactylis glomerata*, cocksfoot; *Poa cita*, tussock grass) was grown with a companion species. Percentage change is the difference to when each species grew alone.

3. Discussion

Measuring nutrient concentrations in foliage provides a surrogate but arguably the most realistic measure of the exploitation of the soil nutrient pool. In the present study, no direct attention was given to the processes in the soil that were responsible for differences in plant uptake. Interactions between plants that take place belowground are often overlooked, even though roots of different species are frequently intermingled, with growth, root exudates [24,25], root turnover [26], death, and decay [27] generally occurring in mixed species rhizospheres. Furthermore, the main input of nutrients to the soil is from root decomposition [28]. Otherwise, nutrients are largely bound to solid phase constituents of the soil with only small proportions entering the soil solution and becoming readily available for plant uptake. Undoubtedly, complex interactions in the rhizosphere affect soil biogeochemistry and nutrient acquisition by plants [24,29], but these were beyond the scope of the experimental work of the present study.

Our results showed that foliar concentrations of P and Mn uptake in proteas and grasses were consistently modified when they were grown together in species combinations, compared to when they were grown alone, but this also extended to elevated foliar concentrations of up to nine other elements (K, Ca, S, Fe, Mg, Zn, Cu, B, and Mo). Our assumption that P acquisition by the cluster-rooted proteas would play a definitive role is evident in the results, in terms of its increased P concentrations in the foliage of pasture grasses (*L. perenne* and *D. glomerata*), together with elevated K and Ca. The tussock grass (*P. cita*) had enhanced amounts of at least five elements (K, Ca, S, Mn, and Zn), but not of P, when growing with proteas. There appeared to be little reciprocation from the tussock grass to proteas. The low-fertility soil probably would have provided more natural conditions for this native grass, which is likely to explain its competitive abilities in procuring deficient nutrients from the soil when it was grown with proteas.

Dactylis glomerata (cocksfoot) provided a better demonstration of species complementary than ryegrass, probably because it grew better and had more biomass. *Dactylis*

provided the most significant impacts on nutrient uptake in the proteas. The two *Grevillea* species with origins in the ancient fertility-depleted soils of Australia benefited substantially through coexistence and the presence of neighbouring grasses in terms of an elevated uptake of most of the range of nutrients. In comparison, a lesser uptake of key nutrients (including Mn, Fe, Zn, and B) by the South African *Protea* when grown together with grasses implies some combination of competitive losses and less sharing, perhaps reflecting an evolutionary history on soils with more adequate levels of fertility, as discussed below. A recent study involved N and P fertilization of two fynbos sites in the Western Cape province of South Africa. Both study areas contained *P. neriifolia* as one of the two dominant species, although both sites had just been cleared of vegetation by wildfires [30]. Compared to six forest tree species, it was found that the thinner root traits of 12 emergent fynbos plants (that did not include proteas) provided a competitive advantage for the procurement of nitrogen, which unexpectedly appeared to be a more significant constraint than P. Nitrogen was largely overlooked in the present study as it appeared to be neither deficient nor a key element in our soil. Furthermore, proteas are not a natural component of vegetation in NZ soils.

There were differences between the *Protea* and the *Grevillea* spp. in terms of foliar nutrient concentrations when grown with grasses. The *Grevillea* spp. and grasses benefited by growing in combination with each other, with both obtaining more P, especially *G. barklyana-Dactylis* combinations. Otherwise, *Grevillea* also procured more S, Mg, Mn, Zn, and B, and the grasses obtained more K and Ca. *Protea neriifolia*-grass combinations were competitive rather than complementary, with the protea apparently less able to procure key deficient elements in the presence of grasses and had a higher foliar uptake of six elements when it was growing alone. There was no obvious benefit to *P. neriifolia* growing with neighbouring grasses.

Likely explanations that would describe the processes responsible for different uptake patterns are to be widely found in the scientific literature. In broad terms, two of the most important ways that root exudates influence nutrient availability and uptake are through organic acid and phytosiderophore secretion [25]. In proteas, the availability of phosphorus in soil is the most important determinant of cluster root formation, and carboxylates exuded from the roots promote P mobilization in the soil [13]. Deficiencies of other elements, including N, K, Mn, and Fe also enhance cluster root development. Graminoid-secreted phytosiderophores release chelators to form complexes with soil metals, increasing metal solubility and mobility, particularly of Fe that is often in abundant but insoluble Fe (III) precipitates in soil. Many phenolics produced in the rhizosphere of dicots can form complexes with metals that may also increase their availability. In low-nutrient environments, plants can produce root exudates as symbiotic signals to soil microbes involved in nutrient procurement, to use extracellular enzymes to release P from organic compounds, and organic acids to solubilize soil Ca, Fe, and Al phosphates [31]. There is increasing evidence that plants can be complementary to one another to procure nutrients more efficiently [32] and at reduced metabolic costs [33]. However, the mechanistic explanations are complex; for example, many phytohormones are involved in interactions between roots, soil, and microbial communities [34]. Rhizosphere processes are insufficiently understood [35], and there remains a paucity of studies that provide mechanistic evidence from soil-based systems [36].

The importance of considering multiple nutrient constraints on plant productivity has been stressed elsewhere [37]. The requirements of plants for similar base concentrations but differing amounts of particular nutrients are likely to be specific to the plant species, and this is probably reflected in the differing foliar concentrations recorded in the present study. The most likely capacity-based approach to nutrient acquisition [29] assumes that plants expend metabolic energy to acquire nutrients by exploiting gradients of nutrient molecules inside and outside the root, using specific nutrient-acquiring proteins, pumps, transporters, and channels [29].

There was some evidence from the present study of transgressive overyielding in the context of an increased proportion of the key nutrients being removed from the total soil pool by combinations of species compared to monocultures. No account was taken of nutrient uptake into the woody or green stems of the proteas in terms of total offtake. Nutrient concentrations in these plant components would be expected to be much lower than in foliage, but the amount of additional nutrients in these fractions could have great relevance to production systems and phytoremediation technologies. The competition for nutrients, facilitation, and complementarity are all major driving forces of ecosystem productivity [35]. In the context of species complementarity, we have shown that species not naturally found together have functional attributes in the rhizosphere that can be shared to facilitate an improved procurement of nutrients.

A better understanding of these functional traits could be very useful in the context of the sustainability of plant communities of native or exotic species, or combinations of both (novel native plant communities) in New Zealand and elsewhere [3,22]. This could be a step towards the better management of vegetation and soils in low-input agricultural systems. More fundamental and applied research knowledge of functional biodiversity and plant species complementarity is required in the context of soil biogeochemistry. The findings of the present study illustrate functional compatibility as well as competition between plant rhizospheres for plant nutrients. Beneficial coexistence appears to be explained by the differences between the plant rhizospheres of different species which exploit different components of the soil nutrient pool [38,39]. This implies that the enhancement of species diversity, for example, beyond simply focusing on legumes and grasses in pasture agronomy [3], may be a better way to manage ecosystems, including production systems, with low-fertility or degraded soils. We suggest that it would be worthwhile to extend the experimental approach used in the present study to a wider range of species combinations that have a direct practical application to less-intensive grazing systems, phytotechnologies, and to the conservation and restoration of biodiversity.

4. Materials and Methods

Soil (1–20 cm depth) was collected from a site in Canterbury (altitude 611 m), South Island, New Zealand (S 43°20′35″, E 171°36′59″), that was described in detail in earlier papers [3,40]. The site was originally forested, probably until the mid-19th century. Since then, the land has been extensively grazed by sheep and wild ruminants but otherwise has been largely undisturbed. Undoubtedly, the soil, which had patchy vegetation cover, was substantially degraded through forest removal, mammalian grazing impacts, exposure, and erosion, probably for a century or more. The collected soil was thoroughly mixed, then air-dried and sieved (2 mm) prior to being used in the experimental work. Samples were analysed using standard methods by Analytical Services, Soils and Physical Sciences Department, Lincoln University (Table 1), showing a range of key determinants (pH, Ca, sulphate-S, soluble P, Cu, Mg, Mn, and B) were less than optimum for plant growth. Available P, Ca, and B were extremely deficient, although there was adequate N for healthy plant growth at yields that could be achieved in the landscape of its origin.

Species were selected from the Proteaceae (proteas) and Poaceae (grasses) as being representative of functional groupings that are known to possess different and contrasting traits of nutrient acquisition in the rhizosphere. We grew three species of proteas: *Grevillea barklyana* F. Muell. Ex Benth. (Gully- or large-leaf grevillea) endemic to south-western Australia; *Grevillea* Robin Hood (a hybrid cultivar of *G. hookeriana* Meisn.), endemic to south-eastern Australia; and *Protea neriifolia* R. Br. (narrow-leaf sugarbush), endemic to the Western and Eastern Cape of South Africa. Fynbos soils are characterised by low soil fertility [41], but dense stands of *P. nerriifolia* are naturally found on less-leached granite-derived renosterveld soils on mountain slopes [42,43] that are more fertile [44]. The inherent fertility is likely to be much lower in the more ancient and strongly weathered soils of Australia [30,45] than in the South African soils. All three species of protea produce cluster roots. The three species only grow ornamentally in New Zealand. These proteas were

grown either alone or in combination with single species of grasses: one of two widespread and common grasses, *Lolium perenne* L. (perennial ryegrass), and *Dactylis glomerata* L. (cocksfoot), or *Poa cita* Edgar (silver tussock) which is an endemic New Zealand tussock grass [46].

Table 1. Analysis of physico-chemical determinants in the experimental soil.

Indicators	Units	Concentration	Typical Range *
pH [1]	pH Units	5.70	5.70–6.20
Total Nitrogen [2]	%	0.46	0.30–0.60
Total Carbon [3]	%	5.80	-
Organic Matter [4]	%	10.0	7.00–17.0
Total Phosphorus	mg kg^{-1}	464	700–1600
Olsen Phosphorus [5]	mg L^{-1}	4.33	20.0–30.0
Potassium [6]	me/100 g	0.49	0.30–0.60
Calcium [6]	me/100 g	2.03	5.00–12.0
Magnesium [7]	me/100 g	0.60	0.60–1.20
Sodium [7]	me/100 g	0.05	0.00–0.30
Sulphate Sulphur [8]	mg kg^{-1}	6.43	10.0–20.0
Iron [7]	mg L^{-1}	84.0	500–1000
Manganese [7]	mg L^{-1}	3.20	8.00–65.0
Zinc [7]	mg L^{-1}	1.75	0.80–4.00
Copper [7]	mg L^{-1}	0.37	0.40–2.00
Boron [7]	mg L^{-1}	0.19	0.60–1.20

* Typical range for agricultural soils in New Zealand. Analyses follow standard methodology from a commercial laboratory. Analyses by the commercial laboratory were routinely carried out by defined volume rather than mass of soil. Method: [1] 1:2 (*v*/*v*) soil:water slurry followed by potentiometric determination of pH. [2] Determined by NIR, calibration based on total N by Dumas combustion. [3] Determined by NIR, calibration based on total Carbon by Dumas combustion. [4] Organic Matter is 1.72 × Total Carbon. [5] Olsen extraction followed by Molybdenum Blue colorimetry. [6] 1 M Neutral ammonium acetate extraction followed by ICP-OES. [7] Mehlich 3 Extraction followed by ICP-OES. [8] 0.02 M Potassium phosphate extraction followed by Ion Chromatography.

A pot trial was set up in a glasshouse at Lincoln University. The cluster root forming species were taken from cuttings of single plants, rooted in seed trays, and then transplanted into 3.5 L plastic pots (15 cm diameter, 20 cm height). Thirteen experimental treatments consisted of three cluster-root forming species and three grasses growing either singly or in combinations, with five replicates per treatment. Pots were arranged in a randomized single block design on a glasshouse bench. Glasshouse temperatures for the duration of the experiment were 19.0 °C (mean); 13.6 °C (min)–34.7 °C (max). Plants were watered sparingly every two days. Survivorship was generally good, but one Gb and one Pn died after transplanting, one Pn (Rg) died after first harvesting, and one Pn (Tg) died a few days before the final harvest.

After 6 months' growth, plant material was sampled for chemical analysis; five leaves were harvested from each of the proteas, and the grasses were harvested to 2 cm above the soil surface. This was repeated 6 months later when the plants were completely harvested, and root systems were separated by careful washing. Aboveground plant material was sorted into separate species, dried (65 °C, 48 h), weighed, and finely ground, microwave digested in 5 M HNO_3, and then chemically analysed by ICP-OES using standard methodology. For statistical analysis, data not normally distributed were log-transformed before analysis. Differences between means were determined using one-way ANOVA, with a post-hoc Fisher LSD test. All analyses were conducted using Minitab 19.

5. Conclusions

This study provided evidence of the compatibility between plant species with contrasting functional rhizosphere traits. Nutrient constraints in the experimental soil were better addressed by combinations of proteas and grasses growing together. Species combinations substantially increased the procurement of key deficient elements, providing evidence that mixed-species rhizospheres enable an improved exploitation of the soil nutrient resource.

This was the result of higher foliar nutrient concentrations and enhanced total uptake of nutrients. The sharing of access to the soil nutrient pool is evident in these findings. This implies that a strategy of competition for plant nutrients may be less important than functional compatibility and mutual enhancement of uptake between neighbouring species in low-fertility or degraded soils.

Author Contributions: All authors contributed to the planning and execution of the project, and to the manuscript preparation. Z.W. carried out the practical work and data analysis as part of his PhD programme supervised by N.D., T.M. and B.R., N.D. and Z.W. are responsible for the final manuscript draft. All authors have read and agreed to the published version of the manuscript.

Funding: This research was partly funded by the Miss E.L. Hellaby Indigenous Grasslands Research Trust (ZW2020), which provided PhD scholarship support for Zhang Wei.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The research team is grateful to Brent Richards, Leona Meachen, Roger Cresswell, Emily Huang, and Hassall Leanne for their practical support.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Nutrient concentrations in protea foliage while each species was growing with grasses (Cf, Cocksfoot; Rg, Ryegrass; Tg, Tussock grass) at 1st and 2nd sampling events. Different letters each indicate significant differences ($p < 0.05$) within each treatment. Bold alphanumerics indicate significant differences to when the proteas were growing alone.

Elements		*Grevillea barklyana*				*Protea neriifolia*				*Grevillea* Robin Hood	
		Alone	**With Rg**	**With Cf**	**With Tg**	**Alone**	**With Rg**	**With Cf**	**With Tg**	**Alone**	**With Cf**
P	1st	1010a	1100a	1170a	1120a	870a	977a	667a	650a	985a	1370a
	2nd	710a	910a	**1430b**	754a	642a	739ab	**1140b**	696a	630a	**1490b**
K	1st	4020a	4450ab	**4790b**	4240a	4900a	4630a	6170a	5050a	7600a	7570a
	2nd	4350a	3950a	4320a	4270a	7920a	5700a	8270a	7340a	6070a	5640a
Ca	1st	10,100a	10,300a	10,800a	10,900a	**13,600a**	10,200b	10,700b	10,000b	11,400a	11,800a
	2nd	9270a	11,200a	10,200a	10,300a	**11,590a**	8180b	9370b	8650b	9210a	10,610a
Mg	1st	1880a	2030a	**2590b**	2040a	2110a	1660a	1750a	1610a	1780a	1910a
	2nd	1050a	1220ab	**1320b**	1150a	1130a	1380a	1310a	1290a	1170a	1320a
S	1st	1290a	1360ab	**1590b**	1330ab	1620a	1150a	946a	901a	1620a	1830a
	2nd	812a	1000a	**1360b**	854a	1300ab	923b	1350a	1020ab	940a	1280a
Fe	1st	115ab	110ab	151a	80.1b	356a	192b	265ab	233ab	98.6a	112a
	2nd	54.9a	58.3a	52.4a	93.8b	33.3a	32.5a	36.7a	46.1a	68.3a	49.5a
Mn	1st	637a	694a	843a	636a	347a	262a	235a	231a	611a	708a
	2nd	429a	**926b**	**679c**	**643c**	325a	216ab	219ab	207b	398a	**910b**
Zn	1st	16.1a	15.0ac	**21.4b**	13.1c	49.6a	27.1a	31.1a	29.4a	16.2a	15.0a
	2nd	8.26a	**14.0b**	**18.7c**	11.6ab	38.2a	17.0b	28.1ab	24.1ab	13.9a	18.9a
Cu	1st	17.9a	16.6ab	19.8a	8.53b	**15.8a**	4.27b	5.79b	4.89b	12.3a	10.2a
	2nd	4.15a	4.27a	4.32a	3.82a	5.11ab	4.03b	5.74a	4.47ab	4.55a	5.17a
B	1st	13.5a	14.3a	**20.2b**	13.7a	17.4a	15.6ab	14.4ab	12.9b	20.1a	13.2b
	2nd	11.1a	12.1ab	**13.5b**	11.5a	21.3a	15.1a	19.1a	16.5a	15.8a	17.6a
Mo	1st	0.16a	0.16a	0.17a	0.13a	0.13	<0.02	0.13	0.12	0.14a	**0.12a**
	2nd	<0.02	0.06	0.14	0.08	0.03a	0.11a	0.02a	0.03a	0.07a	**0.12b**
Ni	1st	1.49a	1.48a	1.08a	1.41a	1.86a	1.26a	1.76a	1.06a	0.97a	1.47b
	2nd	0.87a	0.73a	0.89a	1.07a	0.72a	0.73a	0.67a	0.71a	1.27a	0.70a

Table A2. Nutrient concentration in grass foliage when they were growing alone or with proteas (Gb: *Grevillea barklyana*, Pn; *Protea neriifolia*, GRH; *Grevillea* Robin Hood) at 1st and 2nd sampling events. Different letters each indicate significant differences ($p < 0.05$) within each treatment. Bold alphanumericals indicate significant differences to when the species was growing alone.

Element		Ryegrass			Cocksfoot				Tussock Grass		
		Alone	With Gb	With Pn	Alone	With Gb	With Pn	With GRH	Alone	With Gb	With Pn
P	1st	1010a	1430b	1310ab	1110a	1190a	1390a	1510a	1030a	1060a	1110a
	2nd	477a	**675b**	635ab	412a	501ab	**514b**	**516b**	421a	**552b**	430ab
K	1st	9570a	**12,300b**	35,400b	11,300a	12,700a	39,900b	37,100b	7770a	7160a	**17,100b**
	2nd	17,300a	19,400a	17,900a	19,900a	22,300a	20,500a	23,800a	9840a	**12,600b**	9900a
Ca	1st	6770a	6400a	7630a	6340a	6860a	**8330b**	**7300b**	2990a	**3770b**	3620ab
	2nd	7170a	6460a	7460a	4140a	5760a	6110a	4450a	2640a	3120a	2890a
Mg	1st	3460a	3370a	3660a	2830a	2920a	2590a	2990a	865a	1000a	1250a
	2nd	2870a	2700a	2920a	1170a	1600a	1280a	1390a	684a	660a	866a
S	1st	3190ab	2760b	4030a	2870a	3280a	3310a	3130a	2230a	1600a	2320a
	2nd	2140a	2540a	3220a	1350a	1560a	1440a	1760a	1040a	1290b	1250ab
Fe	1st	222a	247a	265a	128a	97.0a	248a	124a	74.9a	83.2a	82.4a
	2nd	108ab	82.3b	129a	46.6a	52.7a	80.8a	67.2a	138a	50.7a	46.1a
Mn	1st	94.1a	103a	90.1a	287a	351a	364a	320a	105a	**141b**	**121b**
	2nd	197a	125a	147a	201a	263a	396a	270a	108a	116a	77.9a
Zn	1st	50.0a	34.2ab	28.1b	39.4a	34.1a	90.4a	43.3a	22.2a	39.2a	24.1a
	2nd	43.1a	17.3b	24.4b	12.9a	20.1a	25.8a	27.9a	11.0a	**15.3b**	10.7a
Cu	1st	8.23a	10.3a	9.23a	11.8a	11.9a	16.7a	16.9a	8.22a	8.16a	9.83a
	2nd	6.11a	5.63a	6.07a	4.52a	5.59ab	**6.28b**	**5.67b**	4.31a	4.22a	4.42a
B	1st	8.7a	8.07a	7.42a	5.79a	6.71a	6.67a	7.10a	6.27a	5.44a	8.56a
	2nd	10.7a	9.03a	10.1a	7.42a	8.20a	9.51a	5.92a	7.07a	7.81a	6.01a
Mo	1st	0.41a	0.46a	0.43a	0.69a	0.58a	0.66a	0.89a	0.47a	0.53a	0.33a
	2nd	0.20a	0.44a	0.32a	0.21a	0.38a	0.41a	0.36a	0.44a	0.33ab	0.27b
Ni	1st	2.03a	2.05a	2.31a	3.01a	3.36a	3.66a	2.77a	1.88a	1.43a	2.12a
	2nd	2.04a	1.75a	1.59a	1.56a	1.73a	2.50a	3.99a	5.36a	1.18b	1.51ab

Table A3. The total foliar uptake (μg) of each nutrient by each of the six species according to whether they were growing alone or with a companion species. (Gb: *Grevillea barklyana*, Pn; *Protea neriifolia*, G.RH; *Grevillea* Robin Hood, Cf, Cocksfoot; Rg, Ryegrass; Tg, Tussock grass). Different letters each indicate significant differences ($p < 0.05$) within each treatment. Bold alphanumericals indicate significant differences to when the species was growing alone. Minimum detectable limits of Mo (0.02 mg kg^{-1}) were used for uptake calculations of this element.

Species	N	P	K	Ca	Mg	S	Fe	Mn	Zn	Cu	B	Mo	Ni
Gb	**51.3a**	20,600a	127,000a	268,000a	30,500a	23,600ab	1600ab	12,500a	240a	121a	322a	0.58a	25.3a
Gb(Rg)		16,900a	73,900b	206,000a	22,700b	18,900a	1130a	16,600a	255a	79.5b	226b	0.72a	14.1a
Gb(Cf)	40.0b	**31,600b**	94,600ab	22,7000a	29,200ab	30,400b	1150a	15,200a	**410b**	95.0ab	302ab	3.03b	20.3a
Gb(Tg)		18,700a	106,000a	256,,000a	28,500ab	21,200ab	2340b	15,900a	289a	95.2ab	286ab	2.10b	25.6a
Pn	11.2a	6930ab	77,700a	126,000a	12,000a	15,200a	358a	3780a	412a	55.3a	240a	0.23a	8.59a
Pn(Rg)		3570a	25,100a	32,800b	5390a	3840b	131a	853b	76.1b	18.8a	63.5b	0.27a	2.93a
Pn(Cf)	7.30a	12,000b	79,200a	92,900ab	12,100a	12,600ab	366a	2120ab	277ab	55.6a	175ab	0.2a	6.48a
Pn(Tg)		6100ab	66,100a	84,500ab	138,00a	10,000ab	432a	2350ab	220ab	45.3a	150ab	0.23a	7.74a
G.RH	29.8a	10,800a	112,000a	155,000a	20,500a	16,200a	1200a	6610a	257a	80.9a	279a	0.82a	23.3a
G.RH(Cf)	26.3a	**22,400b**	90,200a	15,9000a	20,800a	19,500a	752a	**13,400b**	287a	83.5a	275a	**1.80b**	11.2a
Rg		517a	18,000a	7100a	2850a	2230a	106ab	221a	47.2a	6.36a	10.7a	0.21a	2.15a
Rg(Gb)		691a	20,500a	6950a	2810a	2690a	85.7a	150a	18.7b	5.73a	9.59a	0.62a	1.89a
Rg(Pn)		752a	21,700a	9260a	3580a	3760a	157b	192a	30.1ab	7.33a	12.8a	0.41a	2.00a
Cf		1050a	49,100a	10,300a	2970a	3450a	115a	488a	33.8a	11.1a	19.1a	0.55a	3.96a
Cf (Gb)		899a	38,800a	11,300a	2680a	2600a	92.7a	451a	31.6a	9.56a	16.1a	0.72a	3.20a
CF(Pn)		867a	33,900a	10,300a	2240a	2500a	133a	625a	43.5a	10.6a	16.6a	0.70a	4.43a
Cf (GRH)		913a	44,900a	7410a	2510a	3310a	111a	494a	60.8a	10.5a	10.2a	0.70a	6.84a
Tg		554a	13,400a	3710a	1020ab	1430a	**140a**	152a	15.2a	5.8ab	9.96a	0.57a	**5.36a**
Tg(Gb)		596a	13,600a	3490a	715a	1400a	51.5b	125a	17.0a	4.5b	7.87a	0.38a	1.35b
Tg(Pn)		767a	19,200a	4410a	1460a	2390a	76b	125a	19.0a	7.19a	11.1a	0.53a	2.36b

Table A4. The total uptake of each nutrient (μg) by all of the foliage contained in the pots (species combined), at final sampling, according to whether the six species were growing alone or with a companion species. (Gb: *Grevillea barklyana*, Pn; *Protea neriifolia*, G.RH; *Grevillea* Robin Hood, Cf, Cocksfoot; Rg, Ryegrass; Tg, Tussock grass). Different letters each indicate significant differences ($p < 0.05$) within each block of treatments. Bold alphanumericals indicate significant differences to when the species was growing alone. Minimum detectable limits of Mo (0.02 mg kg^{-1}) were used for uptake calculations of this element.

Species	P	K	Ca	Mg	S	Fe	Mn	Zn	Cu	B	Mo	Ni
Gb	20,600b	127,000a	268,000a	30,500ab	23,600b	1600b	12,500b	240b	121a	322a	0.58cd	25.3a
Gb&Rg	17,600b	94,400b	213,000a	25,500b	21,600b	1210b	16,800a	273b	85.2b	236b	1.34c	16.0ab
Gb&Cf	**32,500a**	133,000a	238,000a	31,900a	**33,000a**	1240b	15,600ab	**442a**	105ab	318a	**3.75a**	23.5a
Gb&Tg	19,300b	120,000ab	260,000a	29,200ab	22,600b	2390a	16,000ab	306b	99.7ab	294ab	2.48b	27.0a
Rg	517c	18,000d	7100b	2850c	2230c	106c	221c	47.2c	6.36c	10.7c	0.21d	2.15c
Cf	1050c	49,100c	10,300b	2970c	3450c	115c	488c	33.8c	11.1c	19.1c	0.55cd	3.96bc
Tg	554c	13,400d	3700b	1020c	1430c	140c	152c	15.2c	5.80c	10.0c	0.57cd	5.36bc
Pn	6930b	77,700ab	126,000a	12,000a	15,200ab	359ab	3780a	412a	55.3ab	240a	0.23b	8.59abc
Pn&Rg	4320bc	46,800bc	42,000bc	8970ab	7600bc	287ab	1050bc	106bc	26.2bc	76.3bc	**0.68a**	4.94bcd
Pn&Cf	**12,800a**	113,000a	103,000a	14,400a	15,100a	499a	2740ab	320a	66.3a	192a	**0.90a**	10.9a
Pn&Tg	6950b	85,300ab	88,900ab	15,300a	12,400ab	524a	2500ab	214ab	53.8ab	161ab	**0.76a**	10.8ab
Rg	517c	18,000c	7100c	2850bc	2230c	106b	221c	47.2bc	6.36c	10.7c	0.21b	2.15d
Cf	1050c	49,100bc	10,300c	2970bc	3450c	115b	488c	33.8bc	11.1c	19.1c	0.55ab	3.96cd
Tg	554c	13,400c	3700c	1020c	1430c	140b	152c	15.2c	5.80c	10.0c	0.57ab	5.36bcd
G.RH	10,800b	112,000ab	155,000a	20,500a	16,200a	1200a	6610b	257a	80.9a	279a	0.82b	23.3a
G.RH&Cf	**23,300a**	13,5000a	167,000a	23,300a	22,800a	863a	**13,900a**	348a	94.0a	285a	**2.50a**	18.0ab
Cf	1050c	49,100b	10,300b	2970b	3450b	115b	488c	33.8b	11.1b	19.1b	0.55b	3.96b

References

1. Meister, A.; Gutierrez-Gines, M.J.; Maxfield, A.; Gaw, S.; Dickinson, N.; Horswell, J.; Robinson, B. Chemical Elements and the Quality of Manuka (*Leptospermum scoparium*) Honey. *Foods* **2021**, *10*, 1670. [CrossRef] [PubMed]
2. Dickinson, N.; Marmiroli, M.; Das, B.; McLaughlin, D.; Leung, D.; Robinson, B. Endemic Plants as Browse Crops in Agricultural Landscapes of New Zealand. *Agroecol. Sustain. Food Syst.* **2015**, *39*, 224–242. [CrossRef]
3. Zhang, W.; Maxwell, T.M.R.; Robinson, B.; Dickinson, N. Legume nutrition is improved by neighbouring grasses. *Plant Soil* **2022**. [CrossRef]
4. Marschner, H. *Mineral Nutrition of Higher Plants*, 2nd ed.; Academic Press: London, UK, 1986; p. 888.
5. Sturludóttir, E.; Brophy, C.; Bélanger, G.; Gustavsson, A.-M.; Jørgensen, M.; Lunnan, T.; Helgadóttir, Á. Benefits of mixing grasses and legumes for herbage yield and nutritive value in Northern Europe and Canada. *Grass Forage Sci.* **2014**, *69*, 229–240. [CrossRef]
6. Schmid, B.; Hector, A.; Saha, P.; Loreau, M. Biodiversity effects and transgressive overyielding. *J. Plant Ecol.* **2008**, *1*, 95–102. [CrossRef]
7. Nyfeler, D.; Huguenin-Elie, O.; Suter, M.; Frossard, E.; Connolly, J.; Luscher, A. Strong mixture effects among four species in fertilized agricultural grassland led to persistent and consistent transgressive overyielding. *J. Appl. Ecol.* **2009**, *46*, 683–691. [CrossRef]
8. Wendling, M.; Buchi, L.; Amosse, C.; Jeangros, B.; Walter, A.; Charles, R. Specific interactions leading to transgressive overyielding in cover crop mixtures. *Agric. Ecosyst. Environ.* **2017**, *241*, 88–99. [CrossRef]
9. Li, L.; Tilman, D.; Lambers, H.; Zhang, F.S. Plant diversity and overyielding: Insights from belowground facilitation of intercropping in agriculture. *New Phytol.* **2014**, *203*, 63–69. [CrossRef]
10. Gliessman, S.R. *Agroecology: The Ecology of Sustainable Food Systems*, 3rd ed.; Taylor & Francis: Boca Raton, FL, USA, 2015; p. 371.
11. Nölke, I.; Tonn, B.; Komainda, M.; Heshmati, S.; Isselstein, J. The choice of the white clover population alters overyielding of mixtures with perennial ryegrass and chicory and underlying processes. *Sci. Rep.* **2022**, *12*, 1155. [CrossRef]
12. An, L.Y.; Pan, Y.H.; Wang, Z.B.; Zhu, C. Heavy metal absorption status of five plant species in monoculture and intercropping. *Plant Soil* **2011**, *345*, 237–245. [CrossRef]
13. Lambers, H.; Finnegan, P.M.; Jost, R.; Plaxton, W.C.; Shane, M.W.; Stitt, M. Phosphorus nutrition in Proteaceae and beyond. *Nat. Plants* **2015**, *1*, 15109. [CrossRef] [PubMed]
14. Neumann, G.; Massonneau, A.; Langlade, N.; Dinkelaker, B.; Hengeler, C.; Romheld, V.; Martinoia, E. Physiological aspects of cluster root function and development in phosphorus-deficient white lupin (*Lupinus albus* L.). *Ann. Bot.* **2000**, *85*, 909–919. [CrossRef]
15. Dinkelaker, B.; Hengeler, C.; Marschner, H. Distribution and function of proteoid roots and other root clusters. *Bot. Acta* **1995**, *108*, 183–200. [CrossRef]
16. Muler, A.L.; Oliveira, R.S.; Lambers, H.; Veneklaas, E.J. Does cluster-root activity benefit nutrient uptake and growth of co-existing species? *Oecologia* **2014**, *174*, 23–31. [CrossRef]
17. Wahl, S.; Ryser, P. Root tissue structure is linked to ecological strategies of grasses. *New Phytol.* **2000**, *148*, 459–471. [CrossRef]

18. Liu, H.; Wu, M.; Chen, J.; Gao, Y.B.; Ren, A.Z. Arbuscular mycorrhizal fungus identity modulates growth effects of endophyte-infected grasses on neighboring plants. *Mycorrhiza* **2020**, *30*, 663–670. [CrossRef]
19. Chen, B.; Shan, X.Q.; Qian, J. Bioavailability index for quantitative evaluation of plant availability of extractable soil trace elements. *Plant Soil* **1996**, *186*, 275–283. [CrossRef]
20. Gross, N.; Suding, K.N.; Lavorel, S.; Roumet, C. Complementarity as a mechanism of coexistence between functional groups of grasses. *J. Ecol.* **2007**, *95*, 1296–1305. [CrossRef]
21. Robinson, B.H.; Anderson, C.W.N.; Dickinson, N.M. Phytoextraction: Where's the action? *J. Geochem. Explor.* **2015**, *151*, 34–40. [CrossRef]
22. Dickinson, N.; Baker, A.; Doronila, A.; Laidlaw, S.; Reeves, R. Phytoremediation of inorganics: Realism and synergies. *Int. J. Phytoremediat.* **2009**, *11*, 97–114. [CrossRef]
23. Robinson, B.H.; Schulin, R.; Nowack, B.; Roulier, S.; Meonon, M.; Clothier, B.; Green, S.; Mills, T. Phytoremediation for the management of metal flux in contaminated sites. *For. Snow Landsc. Res.* **2006**, *80*, 221–234.
24. Coskun, D.; Britto, D.T.; Shi, W.; Kronzucker, H.J. How Plant Root Exudates Shape the Nitrogen Cycle. *Trends Plant Sci.* **2017**, *22*, 661–673. [CrossRef] [PubMed]
25. Bais, H.P.; Weir, T.L.; Perry, L.G.; Gilroy, S.; Vivanco, J.M. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu. Rev. Plant Biol.* **2006**, *57*, 233–266. [CrossRef] [PubMed]
26. Rasmussen, J.; Gylfadóttir, T.; Loges, R.; Eriksen, J.; Helgadóttir, Á. Spatial and temporal variation in N transfer in grass–white clover mixtures at three Northern European field sites. *Soil Biol. Biochem.* **2013**, *57*, 654–662. [CrossRef]
27. Guo, L.B.; Halliday, M.J.; Gifford, R.M. Fine root decomposition under grass and pine seedlings in controlled environmental conditions. *Appl. Soil Ecol.* **2006**, *33*, 22–29. [CrossRef]
28. Prieto, I.; Birouste, M.; Zamora-Ledezma, E.; Gentit, A.; Goldin, J.; Volaire, F.; Roumet, C. Decomposition rates of fine roots from three herbaceous perennial species: Combined effect of root mixture composition and living plant community. *Plant Soil* **2017**, *415*, 359–372. [CrossRef]
29. Tang, J.; Riley, W.J. On the modeling paradigm of plant root nutrient acquisition. *Plant Soil* **2021**, *459*, 441–451. [CrossRef]
30. Lu, M.; Bond, W.J.; Sheffer, E.; Cramer, M.D.; West, A.G.; Allsopp, N.; February, E.C.; Chimphango, S.; Ma, Z.; Slingsby, J.A.; et al. Biome boundary maintained by intense belowground resource competition in world's thinnest-rooted plant community. *Proc. Natl. Acad. Sci. USA* **2022**, *119*, e2117514119. [CrossRef]
31. Dakora, F.D.; Phillips, D.A. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant Soil* **2002**, *245*, 35–47. [CrossRef]
32. Homulle, Z.; George, T.S.; Karley, A.J. Root traits with team benefits: Understanding belowground interactions in intercropping systems. *Plant Soil* **2021**, *471*, 1–26. [CrossRef]
33. Lynch, J.P.; Strock, C.F.; Schneider, H.M.; Sidhu, J.S.; Ajmera, I.; Galindo-Castañeda, T.; Klein, S.P.; Hanlon, M.T. Root anatomy and soil resource capture. *Plant Soil* **2021**, *466*, 21–63. [CrossRef]
34. Lu, Y.Q.; Wang, E.Z.; Tang, Z.Y.; Rui, J.P.; Li, Y.L.; Tang, Z.X.; Dong, W.L.; Liu, X.D.; George, T.S.; Song, A.; et al. Roots and microbiome jointly drive the distributions of 17 phytohormones in the plant soil continuum in a phytohormone-specific manner. *Plant Soil* **2022**, *470*, 153–165. [CrossRef]
35. Hinsinger, P.; Bengough, A.G.; Vetterlein, D.; Young, I.M. Rhizosphere: Biophysics, biogeochemistry and ecological relevance. *Plant Soil* **2009**, *321*, 117–152. [CrossRef]
36. Jones, D.L.; Hodge, A.; Kuzyakov, Y. Plant and Mycorrhizal Regulation of Rhizodeposition. *New Phytol.* **2004**, *163*, 459–480. [CrossRef]
37. Fay, P.A.; Prober, S.M.; Harpole, W.S.; Knops, J.M.H.; Bakker, J.D.; Borer, E.T.; Lind, E.M.; MacDougall, A.S.; Seabloom, E.W.; Wragg, P.D.; et al. Grassland productivity limited by multiple nutrients. *Nat. Plants* **2015**, *1*, 15080. [CrossRef]
38. Franklin, H.M.; Robinson, B.H.; Dickinson, N.M. Plants for nitrogen management in riparian zones: A proposed trait-based framework to select effective species. *Ecol. Manag. Restor.* **2019**, *20*, 202–213. [CrossRef]
39. Hahner, J.L.; Robinson, B.H.; Hong-Tao, Z.; Dickinson, N.M. The phytoremediation potential of native plants on New Zealand dairy farms. *Int. J. Phytoremediat.* **2014**, *16*, 719–734. [CrossRef]
40. Gutiérrez-Ginés, M.J.; Madejón, E.; Lehto, N.J.; McLenaghen, R.D.; Horswell, J.; Dickinson, N.; Robinson, B.H. Response of a pioneering species (*Leptospermum scoparium* JR Forst. & G. Forst.) to heterogeneity in a low-fertility soil. *Front. Plant Sci.* **2019**, *10*, 93. [CrossRef]
41. Richards, M.B.; Cowling, R.M.; Stock, W.D. Soil nutrient dynamics and community boundaries in the Fynbos vegetation of South Africa. *Plant Ecol.* **1997**, *130*, 143–153. [CrossRef]
42. February, E.; Manders, P. Effects of water supply and soil type on growth, vessel diameter and vessel frequency in seedlings of three fynbos shrubs and two forest trees. *S. Afr. J. Bot.* **1999**, *65*, 382–387. [CrossRef]
43. Botha, P.W.; Pauw, A. Rodents and baboons reduce seed cone production of *Protea neriifolia*. *S. Afr. J. Bot.* **2017**, *108*, 303–307. [CrossRef]
44. Heinsohn, R.D.; Pammenter, N.W. Seasonality of shoot growth and flowering in the fynbos shrub *Protea neriifolia* cultivated in a summer rainfall area. *S. Afr. J. Bot.* **1988**, *54*, 440–444. [CrossRef]

45. Lambers, H. *Plant Life on the Sandplains in Southwest Australia: A Global Biodiversity Hotspot*; UWA Publishing: Crawley, WA, USA, 2014; p. 332.
46. Wardle, P. *Vegetation of New Zealand*; Cambridge University Press: Cambridge, UK, 1991; p. 672.