**Title:** Agnostic fungi: plant traits and tissue stoichiometry explain nutrient transfer in common arbuscular mycorrhizal networks of temperate grasslands

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**Abstract:**

Plants and mycorrhizal fungi form close mutualistic relationships that affect the structure and function of ecosystems. Common mycorrhizal networks (many plants associated with the same fungus) can facilitate preferential transfer of carbon and limiting nutrients. The mechanisms behind these networks remain poorly understood. Do common mycorrhizal networks favor fungal growth at the expense of plant resource demands (a fungi-centric view), or are they passive channels through which plants regulate resource fluxes (a plant-centric view)? In experimental restored prairie and introduced pasture systems in the Pacific Northwest, USA, we used stable isotope tracers (13C and 15N), paired with analyses of plant traits and fungal community DNA, to quantify above- and belowground allocation and transfer of carbon and nitrogen between 18 plant species. We measured isotopic enrichment of >1,800 leaves and roots, and found morphological plant? traits and tissue stoichiometry were the most important predictors of interspecific resource transfer. Labeled "donor" plants assimilated isotopic tracers at similar rates; however, nitrogen was preferentially transferred to annual and forb “receiver” plants compared to perennial and grass receiver plants due to differences in tissue stoichiometry. Our findings point to a simple mechanistic answer for long-standing questions regarding mutualism and transfer of resources between plants via mycorrhizal networks.

## Introduction

Plant-mycorrhizal associations are thought to have emerged as rudimentary root systems over 400 million years ago, facilitating the expansion of terrestrial life that followed (Kenrick & Strullu-Derrien, 2014). The transformative power of early fungal symbioses is still evident today in all major plant lineages, from bryophytes to angiosperms, all of which form mycorrhizal connections (van der Heijden et al. 2015). Over 85% of all contemporary flowering plant species form symbioses with fungi, with arbuscular mycorrhizal (AM) associations being the most common (Brundrett 2009). Today, the relationships between plants and AM fungi dominates both managed and unmanaged landscapes and are estimated to be responsible for up to 80% of global primary productivity (van der Heijden et al. 2015). Fungi are gregarious and form partnerships with more than one individual plant (Selosse et al. 2006). By extension, it has been widely hypothesized that the multi-plant-fungal relationships form “common mycorrhizal networks” (CMNs) which facilitate carbon and nutrient transfer between organisms, beyond the immediate plant-fungus mutualism formed by individuals. This relationship is often simplified to the mutual exchange of carbon-based compounds created by plant photosynthesis for limiting soil nutrients mined by fungi (Smith and Read 2008), but is known to exist along a continuum from parasitic to mutualistic (Johnson et al. 1997, Klironomos 2003, Mariotte et al. 2013). A synthesis of empirical research at macro- and micro-levels of ecological organization reveals a gap in understanding of structural and functional properties that could predict how carbon and nutrients are transferred in CMNs (Silva and Lambers 2021).

The literature holds myriad and often complimentary, but sometimes contradictory hypotheses that could explain the CMN mutualism as a key structural and functional component of ecosystems. For example, the “Wood Wide Web” hypothesis emerged from the analysis of isotopically labeled carbon transferred between plants, presumably through fungal mycorrhizae (Simard et al. 1997). This observation set the foundation for economic analogies based on the idea that certain plants which allocate carbon to sustain common fungal symbionts can also benefit from shared nutrients, while plants associating with different mycorrhizal fungi cannot. The “economics” hypothesis (Kiers et al. 2011) proposes that plants and fungi engage in “trades” of nutrients mined by fungi in exchange for carbon-based photosynthates from plants (Fellbaum et al. 2014, Werner and Dubbert 2016, Averill et al. 2019). In this hypothesis, the terms of trade between plant and fungi are mediated by supply and demand for limiting resources, which could

create a dynamic market emerging from interactions between environmental, biochemical, and biophysical variables. Complementing the economic analogy, the "kinship" hypothesis proposes that phylogenetic distance within or across species promotes functional gradients and preferential flow of resources in CMNs (Tedersoo et al. 2020), in which transfer of carbon and nutrients are predicted to be more frequent and abundant between related individuals (e.g., seedlings and trees of the same species) than between unrelated individuals (Pickles et al. 2017).

The past two decades have seen extensive but inconclusive research on these hypotheses and how they relate to empirical measurements of CMN structure and function. There is a lack of alignment between theory and empirical observations. On the one hand, economic analogies suggest that the reciprocally regulated exchange of resources between plants and fungi in CMNs should favor the most beneficial cooperative partnerships (Kiers et al. 2011, Fellbaum et al. 2014). On the other hand, reciprocal transfer is only found in a subset of symbionts under specific conditions, while amplified competition in CMNs is a more common observation (Walder and van der Heijden 2015, Weremijewicz et al. 2016). At the core of this controversy is whether CMNs actively support fungal growth at the expense of plant resource demands (i.e., a fungi-centric view) or function as passive channels through which plants regulate resource fluxes (i.e., a plant-centric view). If plant-centric, we expect to find that the structure and functioning of CMNs give rise to consistent spatiotemporal patterns of resource allocation akin to those predicted by the kinship hypothesis. If fungi-centric, we expect to find that spatiotemporal patterns of resource allocation reflect the composition and functioning of the fungal community regardless of the connecting plant nodes in CMNs. Data exist to support both opposing views (see Silva and Lambers 2021, Figueiredo et al. 2021); therefore, we posit that CMNs are neither plant- nor fungi-centric. Instead, perhaps more than gregarious, AM fungi are "agnostic" with respect to plant species composition and relatedness, and yet affected by major plant functional traits that are known to influence resource use and allocation. This new hypothesis implies that that the rates and direction of resource transfer in CMNs are ultimately a reflection of plant-fungi interactions manifested, for example, in spatiotemporal patterns of resource allocation driven by sink-source strength gradients.

To test the "agnostic fungi" hypothesis, we investigated how interactions among general biophysical and biogeochemical processes operating at the soil-plant-atmosphere interface could explain resource transfer in CMNs better than previous plant- or fungi-centric analogies. We

studied how soil resource-use efficiency and plant traits that regulate physiological performance affect the transfer of carbon and nitrogen in paired experiments where we also sequenced strain-level variation in root fungal DNA, plant community structure, and plant traits to test the effects of relatedness in resource transfer. Our experimental setting includes restored prairie and pasture experimental sites under ambient conditions and rain exclusion shelters, designed to affect soil water and nutrient mass flow, replicated at three different sites across a 520 km latitudinal gradient. Due to the latitudinal and natural climatic difference in communities across sites, not all species were present at all sites (Table S1); however, all "donor" species and all "receiver" functional groups were present at all sites. This allowed us to draw general inferences about the structure and function of arbuscular CMNs in temperate grasslands under a broad range of ecological and environmental conditions. The plants included in these interactions also affect CMN composition and function. For example, Davison et al. (2020) found plant growth form altered AM fungal community and functional diversity. Plant total biomass can also increase nitrogen received through a CMN, an effect that may be compounded by whether plants are woody or less dense grasses (He et al. 2019). This could be explained by larger or denser plants providing more carbon. Both plants and fungi have economic spectra characterized by fast or slow traits and nutrient strategies which together form an interacting continuum potentially driven by N availability (Ward et al. 2022). It is unclear to what extent plant or fungi characteristics drive these plant-fungal interactions. Therefore, we designed an experiment to quantify how plant-fungal interactions influence the structure and functioning of CMNs across broad environmental gradients and resource constraints.

## Methods

We conducted our experiment at three sites situated on a 520 km latitudinal transect that spans three Mediterranean climates: cool, moist (northern site; Tenino, WA) to warm, moist (central site; Eugene, OR) to warm, dry (southern site; Selma, OR). Each circular plot was 3 m in diameter. Half of our plots were restored prairie systems (n = 10 per site) while the other half of the plots were the existing introduced pasture grass community prior to restoration (n = 10 per site). Restored prairie plots were mowed, raked, received herbicide, and seeded in 2014-2015, followed by seeding in fall 2015, 2016, and 2017 (Reed et al. 2019). We erected rainout shelters

that excluded 40% of the rainfall on half the plots at each site (n = 10 rain exclusion, 10 control per site; Fig. 1).

All plants in our system have the potential to form associations with AM fungi (Table S1) (Dickie et al. 2013, Chaudhary et al. 2016, Soudzilovskaia et al. 2020). Previous work demonstrated that the rainout shelters had minimal effects on aboveground community structure or function (Dawson et al. 2022). We labeled perennial plants central to each plot (hereafter, 'donors') and monitored leaf $^{15}N$ and $^{13}C$ for the surrounding plants ('receivers') for up to 21 days. In addition, we sampled roots and soils at 21 days post-labelling. We characterized AM fungal DNA isolated from the root samples, as well as stable isotopes in all leaf and root samples. Our experimental design was nested in a multi-year experiment where in situ data loggers were used to continuously measure variables in all the manipulated plots. We calculated soil matric potentials to account for soil differences between sites (Saxton and Rawls 2006). Rain exclusion only changed soil temperature at the northern site and soil matric potential at the central site (Dawson et al. 2022).

This network of experimental sites was established since 2010 and has been extensively studied since then (Reed et al. 2019, 2021a, 2021b, 2021c, 2022, Peterson et al. 2020) including work on mycorrhizal fungi (Vandegrift et al. 2015, Wilson et al. 2016). Treatment had marginal effects on the soil water potential, which should also affect nutrient uptake through mass flow. Pasture plots were dominated by one to a few species of introduced perennial grasses which we targeted as donors in these plots. We used different species of perennial grass at each site. For restored prairie plots, we targeted the native perennial forb *Sidalcea malviflora ssp. virgata* common to ambient and drought treatments at all sites, and that has shown divergent changes in productivity in response to a warming-induced decline in mycorrhizal colonization attributed to that treatment's drying effect (Wilson et al. 2016). Despite those differences, we did not find significant changes in the average plant community composition or productivity under rain exclusion, which also did not affect morphological and functional traits (e.g., specific leaf area, iWUE, and C:N ratios) of the functional groups we selected for this experiment (Reed et al. 2021c, Dawson et al. 2022).

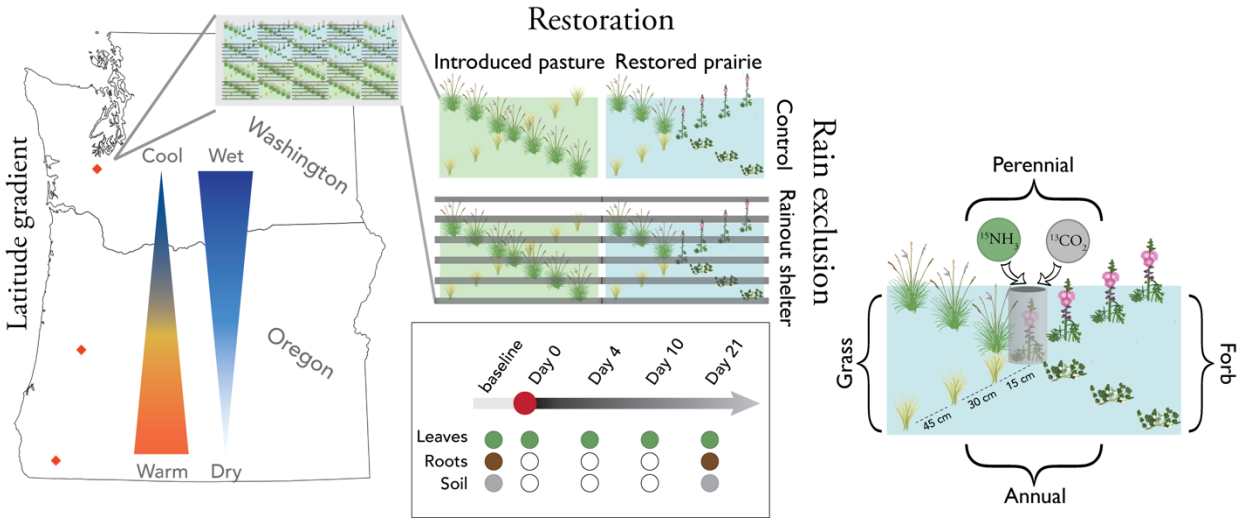


**Figure 1. Schema of experimental set up, sampling, and effects of rainout shelters.**

## Isotopic labelling

At each site, we selected a healthy perennial forb (*Sidalcea malviflora* ssp. *virgata* in restored prairie plots [except in one plot where we used *Eriophyllum lanatum* due to a lack of *S. malviflora ssp. virgata*]), or a grass (*Alopecurus pratensis, Schedonorus arundinaceus,* or *Agrostis capillaris*) in pasture plots at the center of each plot to receive the isotopic labels. On sunny days between 11AM and 3PM, we applied isotopically enriched carbon ($^{13}C$) and nitrogen ($^{15}N$) as a pulse of carbon dioxide ($CO_2$) and ammonia ($NH_3$) to the leaves of target "donor" species common across experimental sites. We performed the labeling experiment using custom-made field-deployable clear chambers with internal fans built to allow gas mixing and fast in situ assimilation of isotopic labels, following established protocols developed in previous isotopically labeling studies (Silva et al. 2015, e.g., Earles et al. 2016, Sperling et al. 2017). We covered the donor plant with a clear plastic cylinder and injected gas in sequence at 20-minute intervals. For $^{13}CO_2$, we made three injections of 2 mL pure $CO_2$ (enriched at 98 atm % $^{13}C$) to double the amount of $CO_2$ in the chamber each time. For $NH_3$, we made two injections of 10 mL pure $NH_3$ (98 atm% $^{15}N$). The dates of application were based on peak greenness calculated as Normalized Different Vegetation Index (NDVI) at each site (see Reed et al. 2019 for details). We sampled leaves from each donor plant immediately after labeling (time point 0) as well as from all plants approximately 4 days (time point 1), 10 days (time point 2), and 21 days (time point 3) post-labelling as logistics permitted (Fig. 1, Table S2). We also collected leaves at time points 1, 2, and 3 from up to twelve plants in each plot representing three replicates of factorial grass/forb

structural groups and annual/perennial life history strategies (Table S1). The number of plants and represented groups depended on which plants were growing in each plot. For example, pasture plots were limited to only grasses and the northern pasture plots had only perennial grasses.

By applying enriched gases only to the aerial portions of established perennial donor plants, we introduced the isotopic tracer to both the plant and mycorrhizal fungal tissues without exposing the soil to the tracers. At the end of the experiment, we harvested entire plants and surrounding rhizospheres at time point 3 and kept them in cool conditions until processing. We separated the roots and rhizospheres, and collected roots from each plant, selecting approximately ten ~3 cm fine root fragments per sample (i.e., third order or finer, where available) for DNA extraction and identification. All roots and rhizosphere soils were stored at -80º C until processing.

**Baseline and Resource Transfer Calculations**

Before isotopic labeling, we collected soil, leaves, and roots from each site. We collected soils in late spring and early summer 2019 to 20 cm depth in each plot. From these soil samples, we removed root fragments that represented the typical roots seen in each plot. We collected leaves for each species in each plot; however, these leaves were contaminated with $^{15}N$ during transport. To replace contaminated samples, we separately sampled leaves from biomass samplings collected in late spring and early summer 2019, ensuring that annual and perennial grasses and forbs were represented at each site.

We oven-dried all samples at 65º C to constant mass and encapsulated them for stable isotope analysis. All stable isotope analysis was done at UC Davis Stable Isotope Facilities using an Elementar Vario EL Cube or Micro Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). We calculated the amount of carbon and nitrogen in each plant compartment (leaves and roots) using standard label recovery equations (Silva et al 2015), using baseline values measured before application of the labelled gases to capture background variations in isotopic composition of unenriched leaves, roots, and soil samples.

205 At each relevant point in space and time, we calculated % nitrogen and % carbon derived from
206 label (%NDFL and %CDFL, respectively) as follows (Kramer et al. 2002, He et al. 2006, Silva
207 2015).
208 **Equation 1**

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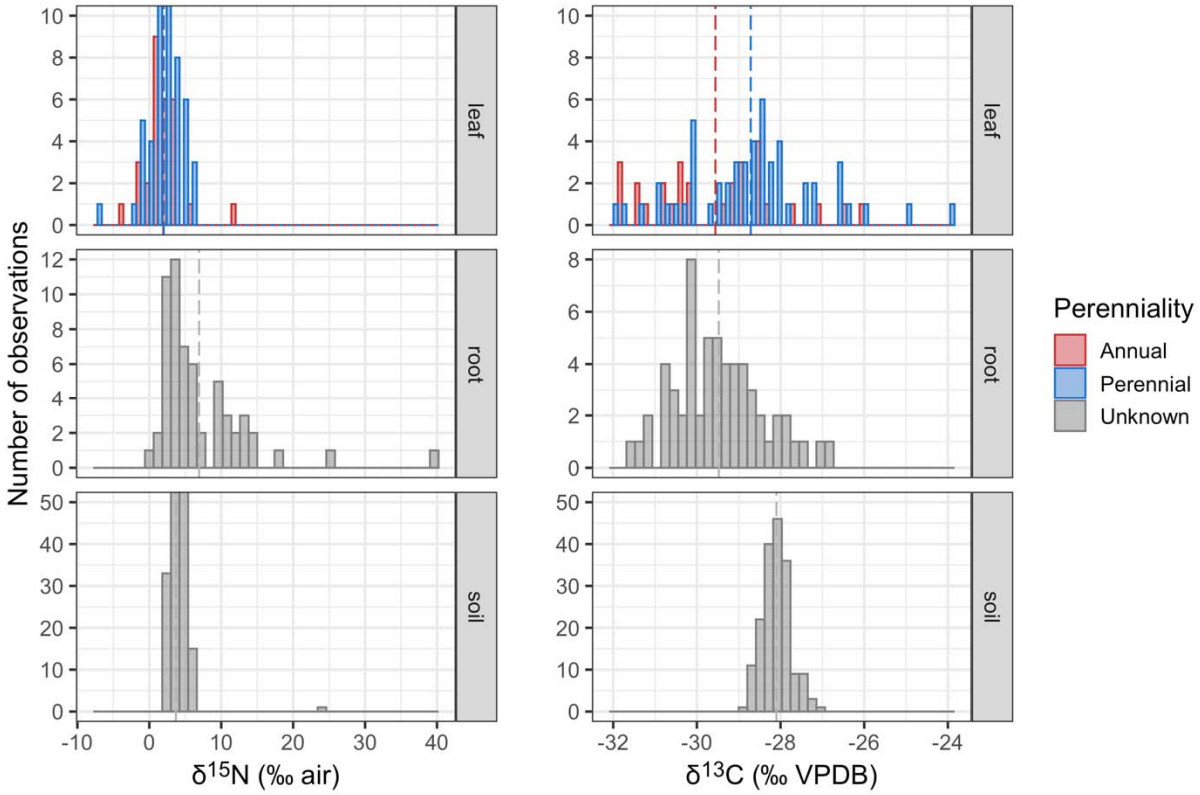
209 Baseline values were calculated from the site- and annual/perennial-specific values for each plant
210 material. Site-specific baseline soil and root isotope ratios represent the whole community
211 because of interconnected rhizospheres where is it was not possible to identify specific species.
212 In all cases, baseline values fell within the expected range for our region (Fig. 2). We calculated
213 intrinsic water-use efficiency following Dawson et al. (2022) using the baseline $^{13}C$ values from
214 the original samples because the contamination only occurred with $^{15}N$.




215
216 **Figure 2. Natural abundance of stable isotopes in leaves, roots, and soil before labelling**.
217 Dashed lines indicate mean value.
218

To better understand post-labelling soil enrichment, we selected a subset of rhizosphere soils that represented six donor plants at each site divided equally between restored prairie and pasture plots, and selected the three most highly $^{15}$N-enriched interspecific receivers in each plot. In addition, we sampled the three most highly enriched interspecific receivers at each site and restored prairie-introduced pasture combination (if they had not been sampled previously). Because pasture plots were sometimes monodominant grasses, we sampled the top three enriched intraspecific receivers at each site and treatment. In total, this came to 48 post-labelling soil samples in 29 plots.

**Fungal analysis**

We extracted DNA from roots of 450 plants harvested at time point 3 (21 days post-label) using Qiagen DNeasy Powersoil HTP kits (Qiagen, Hilden, Germany). We only analyzed DNA from roots, not from the soils collected from each plant's rhizosphere. We characterized each sample's AM fungal composition with a two-step PCR protocol that amplified a ~550bp fragment of the SSU rRNA gene (the most well-supported region for AM fungal taxonomic resolution (Dumbrell et al. 2011)). We used WANDA (5'- CAGCCGCGGTAATTCCAGCT- 3') and AML2 (5'- GAACCCAAACACTTTGGTTTCC-3') primers (Lee et al. 2008, Langmead and Salzberg 2012). We used primers with unique indices so we could multiplex several projects on a single run. We quantified successful PCR amplicons with the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Waltham, MA, USA) on a SpectraMax M5E Microplate Reader (Molecular Devices, San Jose, CA, USA) before purifying with QIAquick PCR Purification kits (Qiagen). We sequenced the purified pools on the Illumina MiSeq platform (paired-end 300bp, Illumina Inc., San Diego, CA, USA) at the University of Oregon Genomics and Cell Characterization Core Facility (Eugene, OR, USA). We used a custom, in-house bioinformatics pipeline to demultiplex reads and filter out duplicate reads generated by PCR duplication using unique molecular identifiers (UMIs) inserted during PCR processing.

We assigned amplicon sequence variants (ASVs) using the dada2 pipeline with standard quality filtering and denoising parameters (Callahan et al. 2016). The dada2 pipeline maintains strain-level diversity at the scale of individual sequence variants rather than clustering sequences into OTUs. This fine-scale measure of fungal sequence diversity was particularly important for our analyses to maintain the greatest chance of detecting a single AM fungal 'individual' in

multiple plant root samples. Taxonomy was assigned to ASVs using the MaarjAM database (2019 release) (Öpik et al. 2010). We used a Bayesian mixture model in the DESeq2 package (Love et al. 2014) to scale ASV counts within and across samples to avoid artificial taxon abundance biases (Anders and Huber 2010).

**Data analysis**

We performed all analyses in R ver. 4.0.4 (R Core team 2015). We removed one plant with $^{15}N$ outlier data. We also removed five plants with mislabeled samples. To meet statistical assumptions, we only included data from plants with successful root fungal DNA extraction. In total, we analyzed data from 389 unique plants: 53 donors and 336 receivers.

We tested the relationship between NDFL and plant traits and site conditions with a mixed-effect ANOVA (Table 1). We constructed a phyloseq object using the ASV table with normalized counts (McMurdie and Holmes 2013), and used iGraph, metagMisc, and RCy3 (Nepusz and Csardi 2006, Mikryukov 2017, Gustavsen et al. 2019) to create networks for each plot. In each network, nodes represented individual plants and edges between nodes represent plants sharing at least one fungal DNA sequence variant. The weighted edges are based on how many fungal ASVs were shared among plants. We calculated degrees of connectivity with tidygraph (Petersen 2022) to examine how many plants each individual plant was 'connected' to (by means of shared fungal ASVs) in each plot (Fig. 3). We also calculated whether each receiver plant shared fungal ASVs with the central donor plant in each plot. We visualized individual plot networks in CytoScape. We visualized shifts in AM fungal community composition using non-metric multi-dimensional scaling (NMDS) in the vegan package, demonstrating the AM fungal community similarity across plants (Oksanen et al. 2022).

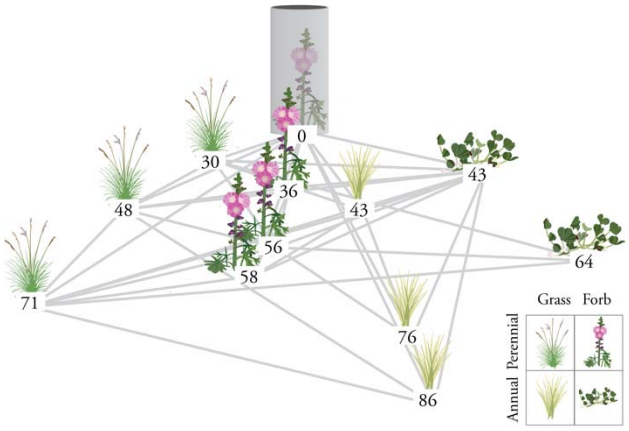


**Figure 3. Example of how networks were constructed for each plot.** The grey cylinder indicates the donor plant for the plot. Numbers beneath the receivers are the distance (in centimeters) from the donor. Degrees were calculated as how many plants each individual plant was connected to by shared fungal ASVs; for example, the perennial grass at 71 cm has 7 degrees.

## Results

Assimilation of isotopic tracers was similar between labeled "donor" plants with no significant differences on average between sites or experimental treatments within sites, including rainfall exclusion or restored status (Fig. S1). At all sites, foliar assimilation of $^{15}N$ and $^{13}C$ by donor plants led to enrichment levels ranging from approximately 5-fold to one order of magnitude higher than baselines, with only a few that were less than 2-fold from baseline. Foliar enrichment levels decreased consistently at all sites and treatments over the 21 day sampling period, suggesting translocation within plants and interspecific transfer between species. We found significant spatial and temporal differences in foliar and root isotope ratios in donors and receivers resulting from interspecific transfer of carbon and nitrogen (Fig. 4; Table 1). Receiver foliar enrichment levels did not correlate with donor foliar enrichment levels within the same plot (Fig. S2).

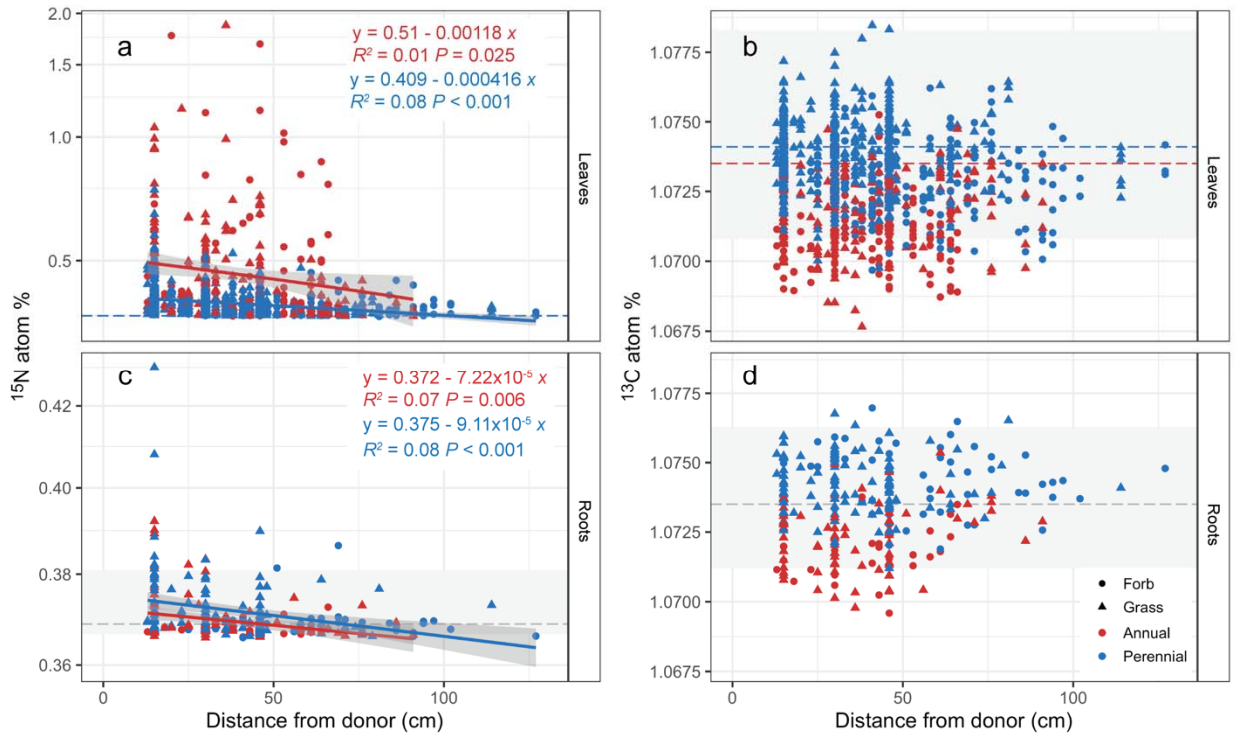



**Figure 4. Decreased receiver enrichment with distance from donor in leaves and roots.** Dashed lines indicate natural abundance means; grey boxes indicate range of natural abundance variation shown in Fig. 2. There is no systematic enrichment of $^{13}C$; however, there is high $^{15}N$ enrichment in leaves. Y-axes are $\log_{10}$ scale. Note that the y-axis scales are different between $^{15}N$ leaves and $^{15}N$ roots. Inset box shows distribution of $^{15}N$ atm% for enriched (greater than natural abundance) annual and perennial leaves and roots.

**Table 1. ANOVA results effects on nitrogen derived from label (NDFL)**

| | $\chi^2$ | P-value |
|---|---|---|
| *Fixed effects* | | |
| **Annual/perennial** | 37.895 | **<0.001** |
| **Grass/forb** | 19.075 | **<0.001** |
| iWUE | 0.150 | 0.698 |
| Degree of connectivity | 0.847 | 0.357 |
| **C:N** | 77.547 | **<0.001** |
| Site | 4.913 | 0.086 |
| Drought treatment | 0.189 | 0.664 |
| Restoration treatment | 2.398 | 0.121 |
| **Distance from donor** | 15.423 | **<0.001** |
| **Time from labelling** | 162.582 | **<0.001** |
| **Annual/perennial:Grass/forb interaction** | 8.670 | **0.003** |
| *Random effect* | | |
| **Plot** | | **<0.001** |

Allocation of $^{13}C$ and $^{15}N$ tracers to roots and subsequent transfer to "receiver" species did not follow expected patterns (e.g., despite donors being perennial, annual receivers were more enriched, indicating that relatedness did not drive the transfer, Fig. 4, Table 1) but varied significantly between functional groups due to their intrinsic differences in physiological traits and tissue stoichiometry (Table 1). We selected 18 representative annual/perennial and grass/forb species of receiver plants, which revealed significant differences between functional groups for NDFL (Fig. 5) but no detectable CDFL relative to baseline (Fig. 4).

Rain exclusion treatment, restoration treatment, and site did not affect interspecific transfer of nitrogen (Fig S3; ANOVA, $P > 0.05$, Table 1), and carbon was not enriched enough to

test transfer (Fig. 4). We did, however, observe significant differences in nitrogen transfer by functional group (Table 1), mirroring intrinsic differences in tissue stoichiometry and iWUE (Fig. 5), despite no significant enrichment in soils collected from the rhizosphere of those same plants (Fig. S4). C:N affected NDFL (Table 1), but NDFL did not correlate with C:N or iWUE (Fig. 5). We did detect a low level of soil enrichment in 4 out of 23 donor soil samples (ranging from 0.382 to 0.479 atm% $^{15}$N).

Annuals had greater $^{15}$N foliar enrichment compared to perennials (ANOVA, $P < 0.001$, Tables 1 and 2). Foliar enrichment decreased over both time and space (ANOVA $P < 0.001$; Fig. 4, Fig. S1). On average, annuals had a lower leaf nitrogen content and higher C:N than perennials (Table 2, Fig. 5). Forbs had higher NDFL than grasses (ANOVA, $P < 0.001$, Table 1) as well as a lower C:N. There was a significant interaction between annual/perennial and grass/forb form (ANOVA, $P = 0.003$, Table 1).

**Table 2. Nitrogen derived from label (NDFL) and leaf tissue nitrogen (% N) four days after labeling**.

| | | | NDFL | | | | | % N | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ***n*** | ***Mean*** | **±** | ***SD*** | ***Min*** | ***Max*** | ***Mean*** | **±** | ***SD*** | ***Min*** | ***Max*** |
| **Annual** | **Forb** | 54 | 0.206 | ± | 0.281 | 0.003 | 1.427 | 1.731 | ± | 0.849 | 0.528 | 4.081 |
| | **Grass** | 93 | 0.130 | ± | 0.199 | 0.001 | 1.534 | 1.233 | ± | 0.919 | 0.359 | 8.004 |
| **Perennial** | **Forb** | 67 | 0.033 | ± | 0.026 | 0.006 | 0.144 | 2.521 | ± | 0.753 | 1.079 | 4.136 |
| | **Grass** | 148 | 0.040 | ± | 0.028 | 0.005 | 0.147 | 1.600 | ± | 0.529 | 0.614 | 2.938 |

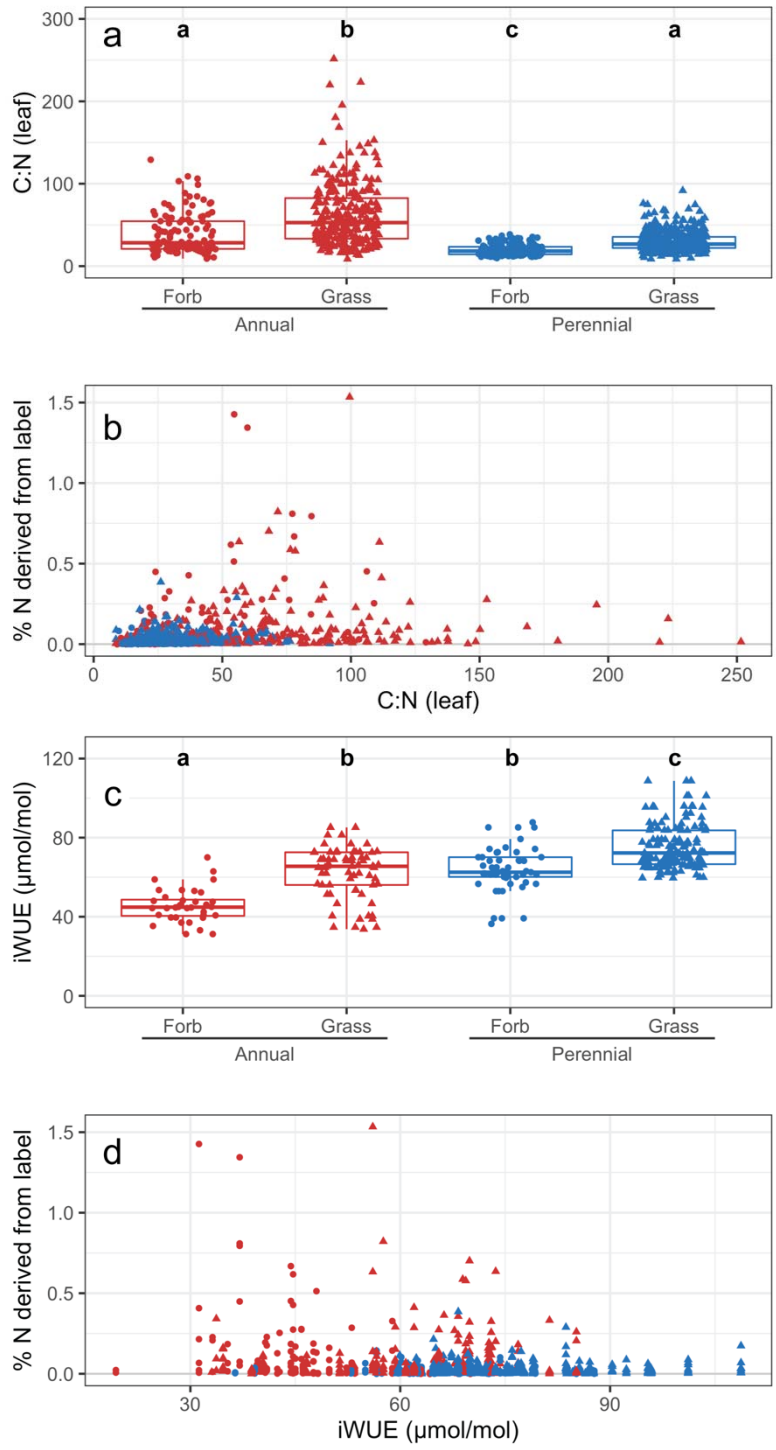



**Figure 5. Stoichiometric and functional traits compared to nitrogen derived from transfer.** A) Leaf C:N by annual/perennial. B) Percent $^{15}N$ derived from label (DFL) compared to C:N in leaves. C) iWUE by annual/perennial as measured before labelling. D) Percent $^{15}N$ DFL compared to iWUE in leaves at all time points.

Our analysis of fungal community composition shows a high degree of connectivity between plants of different species but no obvious pattern of connectedness that could explain preferential nutrient transfer by plant functional groups. Overall, we inferred that plants in all experimental plots and sites were highly 'connected' (as inferred from shared fungal ASVs) because we found that 97.25 % ± 8.01 (SD) of all plants roots within each experimental plot shared at least one fungal DNA sequence variant (ASV) with another plant of the same plot. Fungal community composition was similar across plant functional groups (Fig. 6). Annual plants shared fungi with more plants in the same plot (4.74 plants ± 2.62 SD) compared to perennials (4.04 plants ± 2.49 SD ; t-test, P = 0.019; Table S3), but degrees of connectivity did not predict nitrogen transfer (Table 1). Seventy-three percent of plants were colonized by four or fewer fungi and shared fungi with five or fewer other plants in the plot, making it difficult to determine if strength of connectivity altered nitrogen transfer (Fig. S5).

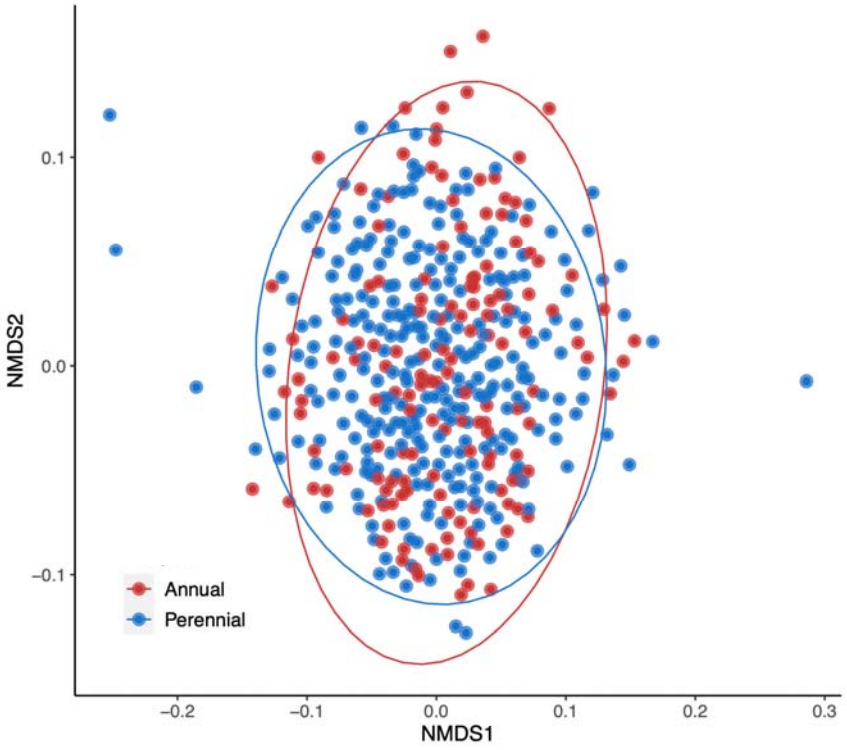



**Figure 6. NMDS of fungal communities**. Each point is an individual plant ordinated by its fungal community.

## Discussion

In our extensively replicated spatiotemporal isotopic tracer experiment, the assimilation and allocation of limiting resources in CMNs was neither plant- nor fungi-centric. Our data show that AM fungi are "agnostic" with respect to plant species composition and relatedness, and that the transfer of nitrogen (the most important nutrient limiting plant growth in our system) is regulated by major functional traits that are known to influence resource use and allocation in plant communities. The rates and direction of resource transfer in CMNs, inferred from pulse labeling and recovery of $^{15}N$ in leaves and rhizospheres, can be predicted from plant traits and distance from donor species (Fig 1). Across all sites and treatments, we observed a stronger sink for $^{15}N$ in annual plants close to the source donor, indicating preferential transfer of limiting resources to that functional group of plants. This observation is contrary to the expectation of the kinship hypothesis that preferential transfer would be expected to occur among perennial donors and receivers. Although plants shared a high proportion of fungal ASVs in their roots (Fig. 6), connectivity did not predict $^{15}N$ transfer (Table 1), and thus we found no evidence for a fungi-centric hypothesis based on which all connected plants would have been expected to be equally enriched in $^{15}N$. In summary, our data suggests that the rates and direction of resource transfer in CMNs are ultimately a reflection of plant-fungi interactions manifested in spatiotemporal patterns of resource allocation driven by plant functional traits and sink-source strength gradients.

We did not find $^{13}C$ enrichment in most samples, above- or belowground, and both $^{15}N$ and $^{13}C$ signatures of receiver plants were independent of donor or soil enrichment levels. We designed this experiment to be informed by previous hypotheses on how carbon and nitrogen transfer occurs in highly connected CMNs, where a dilution of the applied $^{13}C$ label is to be expected given the vast amounts of carbon in the soil and plant biomass. We conducted repeated spatiotemporal sampling of isotopic enrichment levels at increasing distances from donor species, days to weeks after labelling, and in well-established communities exposed to multiple years of experimental treatments, expecting to find evidence of kinship (i.e., greatest resource transfer in related plants), driven by CMN economics (i.e., $^{15}N$ transfer rates coinciding with $^{13}C$ investment in root and fungal mass). Our donor plants were perennials while annuals received, on average, an order of magnitude higher enrichment. Thus, we discarded kinship as a possible driver of transfer in this system. We also did not find evidence of a relationship between $^{15}N$ in leaves and $^{13}C$ in roots. Therefore, here too our data do not support either hypothesis and instead

suggest AM fungi are "agnostic" with respect to plant species partnerships, forming CMNs where the rates and direction of resource transfer ultimately reflects a sink-source strength in ecophysiological performance and stoichiometric gradients.

Our dual-isotope ($^{13}C$ and $^{15}N$) labelling approach was deliberately imposed upon an existing climate experiment to investigate trade between carbon and nitrogen from assimilation to translocation among plant compartments and fungal partners. Our results are consistent with earlier experiments performed in greenhouse experiments under low stress (e.g., temperature controlled and irrigated twice daily) (Silva et al. 2015). However, post-assimilation translocation did not support previous data. Plants acquire $CO_2$ and $NH_3$ from the atmosphere and release those same gases into their surroundings, exhibiting a foliar compensation point at which the evolution of gases is equal to assimilation (Farquhar et al. 1980). This compensation point depends on the partial pressure of $CO_2$ or $NH_3$ in the mesophyll, and therefore on its partial pressure in the atmosphere, with an increase in leaf uptake expected for both gases as their concentration rises. Our pulse experiment worked for both gases, causing lasting enrichment levels in the leaves of donor species and, over time, in the leaves of receiver individuals of other species, suggesting translocation and transfer (Fig. 4 and S1). This result represents an integrated measure of the total foliar assimilation of $NH_3$ and $CO_2$ after a single pulse of isotopically enriched gases.

Nitrogen enrichment levels remained high in leaves and many roots at the end of the experiment, allowing us to measure NDFL across the community and infer the main drivers of N transfer. However, carbon enrichment levels faded before plants were harvested approximately 21 days post-labelling, either due to losses via respiration or redistribution in CMNs where it became undetectable in all but a few cases. After controlling for variation in assimilation rates, we found that annual plants received greater $^{15}N$ enrichment than perennial plants. Plants closest to the donor were most enriched, and $^{15}N$ enrichment decreased over time (Fig. 4). Plant connectivity through a possible CMN did not predict $^{15}N$ enrichment. We did not detect $^{13}C$ enrichment in roots, shoots, or soils. Annuals had lower total nitrogen content than perennials, mirroring intrinsic differences in stoichiometry and water-use efficiency (although with no significant correlation found; Fig. 5), indicating that kinship did not drive this transfer as all donor plants were perennials. Although the rainout shelters had limited effect, there were major

differences across the latitudinal gradient represented by the sites in temperature and soil moisture availability (some HOPS ref.); however, neither treatment nor site affected our results.

The major drivers of differences in allocation of $^{13}C$ and $^{15}N$ to roots and subsequent transfer to "receiver" species were the intrinsic difference in physiological traits and tissue stoichiometry between structural groups (annual/perennial or grass/forb; Table 1). This result points to a simple mechanistic explanation to reconcile long-standing questions regarding mutualism and hierarchical transfer of resources between plants via mycorrhizal networks, an explanation that can lead to general predictions of preferential flow of limiting resources in other ecosystems. For example, previous studies in northern California under environmental conditions similar to those found in our southernmost experimental site showed rapid (days to weeks) transfer of $^{15}N$ applied to the leaves of ectomycorrhizal pines to surrounding annual AM plant receivers (He et al. 2006). Those results were interpreted as evidence for agnostic CMNs because "direct fungal connections are not necessary for N transfer among plants" and "leaves of the annual plants had greater $^{15}N$ derived from source (NDFS) and were more enriched ($^{15}N$ at % excess and $\delta^{15}N$ values) than perennial receivers, irrespective of the mycorrhizal type." Similarly, as proposed by He et al. (2006), our observation of agnostic $^{15}N$ transfer from donor to receivers suggests that annual plants, with their extensive root systems, were a strong sink for N which could be explained by stoichiometric gradients that affect root exudation and recapture of N-containing materials from rhizodeposition. Our data corroborate rapid agnostic transfer among AM plants, with no detectable enrichment in root or soil $^{13}C$ near roots 21 days post-labelling, but do not allow us to determine which mechanism is responsible for the $^{15}N$ transfers.

We inferred a high connectivity between plants within each given treatment and site given the highly similar fungal composition in the root systems of both perennial and annual plants (Fig. 6). (Given the constraints of ASV-identified data, we did this analysis on a strain-level scale and we acknowledge there is a chance that separate spores of the same ASV may have separately infected plants within the same plot. However, we are reasonably confident in our use of fungal ASVs as a proxy for connectivity given the strong overlap in our community and because individuals of one ASV can anastomose in the soil (Mikkelsen et al. 2008).) This overlap could explain the lack of support for the kinship hypothesis in our dataset and offers further support for stoichiometric gradients as the fundamental control of terms of trade in CMNs. The marketplace hypothesis proposes that host plants provide the mycorrhizal fungus

with carbon in the form of simple sugars. The rate which fungi take up these sugars is controlled by their affinity to the host. Different C sources from a host trigger changes in fungal monosaccharide transporter gene expression, causing fungi to increase N uptake from the soil (Fellbaum et al. 2012). However, host and fungus-specific gene expression differences would be weak in our study sites because our DNA results demonstrate that our plants were highly connected by shared arbuscular mycorrhizal (AM) fungal ASVs. In our case, the $^{15}N$ we applied to leaves could have mineralized, been recycled at the soil/fungal interface, and converted into basic organic compounds such as amino acids (e.g., via glutamine synthetase or argininosuccinate synthase) which act as charge balance in the catabolic arm of the urea cycle. The fact that we supplied a carbon source (acetate) independent from the C supply of the host could have reduced N transport in the AM symbiosis. Apoplastic transport would then explain how some of the labeled C ended up in plants even though most of it is expected to go to the fungal symbionts. This mechanism also explains how N and mineral elements (e.g., P) are transferred through CMNs from plant to plant even though they are not expected to limit fungal growth (Ward et al. 2022).

In conclusion, we found that plant-soil stoichiometric gradients and functional traits were the strongest drivers of resource sharing in grassland CMNs. We interpret this finding as evidence of biochemical and biophysical sinks, in which nutrients are allocated to plants with the greatest need for those nutrients, either through a 'passive' mycorrhizal network or direct uptake from soil, or that nutrients should be allocated through water flow. Expanding on previous studies, we propose that agnostic AM fungi facilitate spatiotemporal dynamics of carbon and nitrogen through CMNs in was that are neither plant- nor fungi-centric. That is, plants and fungi that are located closer together in space and with stronger demand for resources over time are more likely to receive larger amounts of those limiting resources.

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## Data availability statement

Data used in these analyses are available online at the Data Dryad repository (https://doi.org/10.5061/dryad.7pvmcvdxt). While this paper is under review, data can be accessed using the following unpublished link:

https://datadryad.org/stash/share/bz0dQHa9xnzgOqwsF_3N0TSx3Oh6OWmElTExtAjyGUc

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