1 **Title:** Agnostic fungi: plant traits and tissue stoichiometry explain nutrient transfer in common

2 arbuscular mycorrhizal networks of temperate grasslands

3

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15

16 **Abstract:**

17 Plants and mycorrhizal fungi form close mutualistic relationships that affect the structure and

18 function of ecosystems. Common mycorrhizal networks (many plants associated with the same

19 fungus) can facilitate preferential transfer of carbon and limiting nutrients. The mechanisms

20 behind these networks remain poorly understood. Do common mycorrhizal networks favor

21 fungal growth at the expense of plant resource demands (a fungi-centric view), or are they

22 passive channels through which plants regulate resource fluxes (a plant-centric view)? In

23 experimental restored prairie and introduced pasture systems in the Pacific Northwest, USA, we

24 used stable isotope tracers (13C and 15N), paired with analyses of plant traits and fungal

25 community DNA, to quantify above- and belowground allocation and transfer of carbon and

26 nitrogen between 18 plant species. We measured isotopic enrichment of >1,800 leaves and roots,

27 and found morphological plant? traits and tissue stoichiometry were the most important

28 predictors of interspecific resource transfer. Labeled "donor" plants assimilated isotopic tracers

29 at similar rates; however, nitrogen was preferentially transferred to annual and forb "receiver"

30 plants compared to perennial and grass receiver plants due to differences in tissue stoichiometry.

31 Our findings point to a simple mechanistic answer for long-standing questions regarding

32 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

64   create a dynamic market emerging from interactions between environmental, biochemical, and

65   biophysical variables. Complementing the economic analogy, the "kinship" hypothesis proposes

66   that phylogenetic distance within or across species promotes functional gradients and preferential

67   flow of resources in CMNs (Tedersoo et al. 2020), in which transfer of carbon and nutrients are

68   predicted to be more frequent and abundant between related individuals (e.g., seedlings and trees

69   of the same species) than between unrelated individuals (Pickles et al. 2017).

70   The past two decades have seen extensive but inconclusive research on these hypotheses

71   and how they relate to empirical measurements of CMN structure and function. There is a lack of

72   alignment between theory and empirical observations. On the one hand, economic analogies

73   suggest that the reciprocally regulated exchange of resources between plants and fungi in CMNs

74   should favor the most beneficial cooperative partnerships (Kiers et al. 2011, Fellbaum et al.

75   2014). On the other hand, reciprocal transfer is only found in a subset of symbionts under

76   specific conditions, while amplified competition in CMNs is a more common observation

77   (Walder and van der Heijden 2015, Weremijewicz et al. 2016). At the core of this controversy is

78   whether CMNs actively support fungal growth at the expense of plant resource demands (i.e., a

79   fungi-centric view) or function as passive channels through which plants regulate resource fluxes

80   (i.e., a plant-centric view). If plant-centric, we expect to find that the structure and functioning of

81   CMNs give rise to consistent spatiotemporal patterns of resource allocation akin to those

82   predicted by the kinship hypothesis. If fungi-centric, we expect to find that spatiotemporal

83   patterns of resource allocation reflect the composition and functioning of the fungal community

84   regardless of the connecting plant nodes in CMNs. Data exist to support both opposing views

85   (see Silva and Lambers 2021, Figueiredo et al. 2021); therefore, we posit that CMNs are neither

86   plant- nor fungi-centric. Instead, perhaps more than gregarious, AM fungi are "agnostic" with

87   respect to plant species composition and relatedness, and yet affected by major plant functional

88   traits that are known to influence resource use and allocation. This new hypothesis implies that

89   that the rates and direction of resource transfer in CMNs are ultimately a reflection of plant-fungi

90   interactions manifested, for example, in spatiotemporal patterns of resource allocation driven by

91   sink-source strength gradients.

92   To test the "agnostic fungi" hypothesis, we investigated how interactions among general

93   biophysical and biogeochemical processes operating at the soil-plant-atmosphere interface could

94   explain resource transfer in CMNs better than previous plant- or fungi-centric analogies. We

95   studied how soil resource-use efficiency and plant traits that regulate physiological performance

96   affect the transfer of carbon and nitrogen in paired experiments where we also sequenced strain-

97   level variation in root fungal DNA, plant community structure, and plant traits to test the effects

98   of relatedness in resource transfer. Our experimental setting includes restored prairie and pasture

99   experimental sites under ambient conditions and rain exclusion shelters, designed to affect soil

100   water and nutrient mass flow, replicated at three different sites across a 520 km latitudinal

101   gradient. Due to the latitudinal and natural climatic difference in communities across sites, not all

102   species were present at all sites (Table S1); however, all "donor" species and all "receiver"

103   functional groups were present at all sites. This allowed us to draw general inferences about the

104   structure and function of arbuscular CMNs in temperate grasslands under a broad range of

105   ecological and environmental conditions. The plants included in these interactions also affect

106   CMN composition and function. For example, Davison et al. (2020) found plant growth form

107   altered AM fungal community and functional diversity. Plant total biomass can also increase

108   nitrogen received through a CMN, an effect that may be compounded by whether plants are

109   woody or less dense grasses (He et al. 2019). This could be explained by larger or denser plants

110   providing more carbon. Both plants and fungi have economic spectra characterized by fast or

111   slow traits and nutrient strategies which together form an interacting continuum potentially

112   driven by N availability (Ward et al. 2022). It is unclear to what extent plant or fungi

113   characteristics drive these plant-fungal interactions. Therefore, we designed an experiment to

114   quantify how plant-fungal interactions influence the structure and functioning of CMNs across

115   broad environmental gradients and resource constraints.

116

117   **Methods**

118   We conducted our experiment at three sites situated on a 520 km latitudinal transect that

119   spans three Mediterranean climates: cool, moist (northern site; Tenino, WA) to warm, moist

120   (central site; Eugene, OR) to warm, dry (southern site; Selma, OR). Each circular plot was 3 m in

121   diameter. Half of our plots were restored prairie systems (n = 10 per site) while the other half of

122   the plots were the existing introduced pasture grass community prior to restoration (n = 10 per

123   site). Restored prairie plots were mowed, raked, received herbicide, and seeded in 2014-2015,

124   followed by seeding in fall 2015, 2016, and 2017 (Reed et al. 2019). We erected rainout shelters

125   that excluded 40% of the rainfall on half the plots at each site (n = 10 rain exclusion, 10 control

126   per site; Fig. 1).

127   All plants in our system have the potential to form associations with AM fungi (Table S1)

128   (Dickie et al. 2013, Chaudhary et al. 2016, Soudzilovskaia et al. 2020). Previous work

129   demonstrated that the rainout shelters had minimal effects on aboveground community structure

130   or function (Dawson et al. 2022). We labeled perennial plants central to each plot (hereafter,

131   'donors') and monitored leaf ^{15}N and ^{13}C for the surrounding plants ('receivers') for up to 21

132   days. In addition, we sampled roots and soils at 21 days post-labelling. We characterized AM

133   fungal DNA isolated from the root samples, as well as stable isotopes in all leaf and root

134   samples. Our experimental design was nested in a multi-year experiment where in situ data

135   loggers were used to continuously measure variables in all the manipulated plots. We calculated

136   soil matric potentials to account for soil differences between sites (Saxton and Rawls 2006). Rain

137   exclusion only changed soil temperature at the northern site and soil matric potential at the

138   central site (Dawson et al. 2022).

139   This network of experimental sites was established since 2010 and has been extensively

140   studied since then (Reed et al. 2019, 2021a, 2021b, 2021c, 2022, Peterson et al. 2020) including

141   work on mycorrhizal fungi (Vandegrift et al. 2015, Wilson et al. 2016). Treatment had marginal

142   effects on the soil water potential, which should also affect nutrient uptake through mass flow.

143   Pasture plots were dominated by one to a few species of introduced perennial grasses which we

144   targeted as donors in these plots. We used different species of perennial grass at each site. For

145   restored prairie plots, we targeted the native perennial forb *Sidalcea malviflora ssp. virgata*

146   common to ambient and drought treatments at all sites, and that has shown divergent changes in

147   productivity in response to a warming-induced decline in mycorrhizal colonization attributed to

148   that treatment's drying effect (Wilson et al. 2016). Despite those differences, we did not find

149   significant changes in the average plant community composition or productivity under rain

150   exclusion, which also did not affect morphological and functional traits (e.g., specific leaf area,

151   iWUE, and C:N ratios) of the functional groups we selected for this experiment (Reed et al.

152   2021c, Dawson et al. 2022).
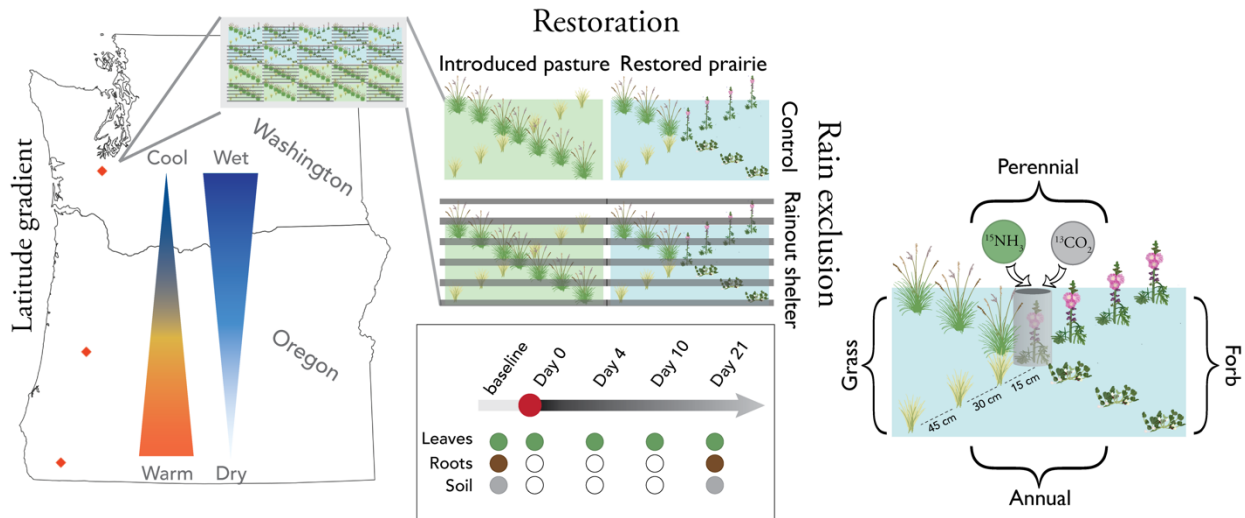
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154 **Figure 1. Schema of experimental set up, sampling, and effects of rainout shelters.**

155

156 **Isotopic labelling**

157   At each site, we selected a healthy perennial forb (*Sidalcea malviflora* ssp. *virgata* in

158 restored prairie plots [except in one plot where we used *Eriophyllum lanatum* due to a lack of *S.*

159 *malviflora ssp. virgata*]), or a grass (*Alopecurus pratensis, Schedonorus arundinaceus,* or

160 *Agrostis capillaris*) in pasture plots at the center of each plot to receive the isotopic labels. On

161 sunny days between 11AM and 3PM, we applied isotopically enriched carbon (^{13}C) and nitrogen

162 (^{15}N) as a pulse of carbon dioxide (CO_2) and ammonia (NH_3) to the leaves of target "donor"

163 species common across experimental sites. We performed the labeling experiment using custom-

164 made field-deployable clear chambers with internal fans built to allow gas mixing and fast in situ

165 assimilation of isotopic labels, following established protocols developed in previous isotopically

166 labeling studies (Silva et al. 2015, e.g., Earles et al. 2016, Sperling et al. 2017). We covered the

167 donor plant with a clear plastic cylinder and injected gas in sequence at 20-minute intervals. For

168 $^{13}CO_2$, we made three injections of 2 mL pure CO_2 (enriched at 98 atm % ^{13}C) to double the

169 amount of CO_2 in the chamber each time. For NH_3, we made two injections of 10 mL pure NH_3

170 (98 atm% ^{15}N). The dates of application were based on peak greenness calculated as Normalized

171 Different Vegetation Index (NDVI) at each site (see Reed et al. 2019 for details). We sampled

172 leaves from each donor plant immediately after labeling (time point 0) as well as from all plants

173 approximately 4 days (time point 1), 10 days (time point 2), and 21 days (time point 3) post-

174 labelling as logistics permitted (Fig. 1, Table S2). We also collected leaves at time points 1, 2,

175 and 3 from up to twelve plants in each plot representing three replicates of factorial grass/forb

176　structural groups and annual/perennial life history strategies (Table S1). The number of plants

177　and represented groups depended on which plants were growing in each plot. For example,

178　pasture plots were limited to only grasses and the northern pasture plots had only perennial

179　grasses.

180　　By applying enriched gases only to the aerial portions of established perennial donor

181　plants, we introduced the isotopic tracer to both the plant and mycorrhizal fungal tissues without

182　exposing the soil to the tracers. At the end of the experiment, we harvested entire plants and

183　surrounding rhizospheres at time point 3 and kept them in cool conditions until processing. We

184　separated the roots and rhizospheres, and collected roots from each plant, selecting

185　approximately ten ~3 cm fine root fragments per sample (i.e., third order or finer, where

186　available) for DNA extraction and identification. All roots and rhizosphere soils were stored at -

187　80º C until processing.

188

189　**Baseline and Resource Transfer Calculations**

190　　Before isotopic labeling, we collected soil, leaves, and roots from each site. We collected

191　soils in late spring and early summer 2019 to 20 cm depth in each plot. From these soil samples,

192　we removed root fragments that represented the typical roots seen in each plot. We collected

193　leaves for each species in each plot; however, these leaves were contaminated with ^{15}N during

194　transport. To replace contaminated samples, we separately sampled leaves from biomass

195　samplings collected in late spring and early summer 2019, ensuring that annual and perennial

196　grasses and forbs were represented at each site.

197　　We oven-dried all samples at 65º C to constant mass and encapsulated them for stable

198　isotope analysis. All stable isotope analysis was done at UC Davis Stable Isotope Facilities using

199　an Elementar Vario EL Cube or Micro Cube elemental analyzer (Elementar Analysensysteme

200　GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer

201　(Sercon Ltd., Cheshire, UK). We calculated the amount of carbon and nitrogen in each plant

202　compartment (leaves and roots) using standard label recovery equations (Silva et al 2015), using

203　baseline values measured before application of the labelled gases to capture background

204　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**

_____

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.
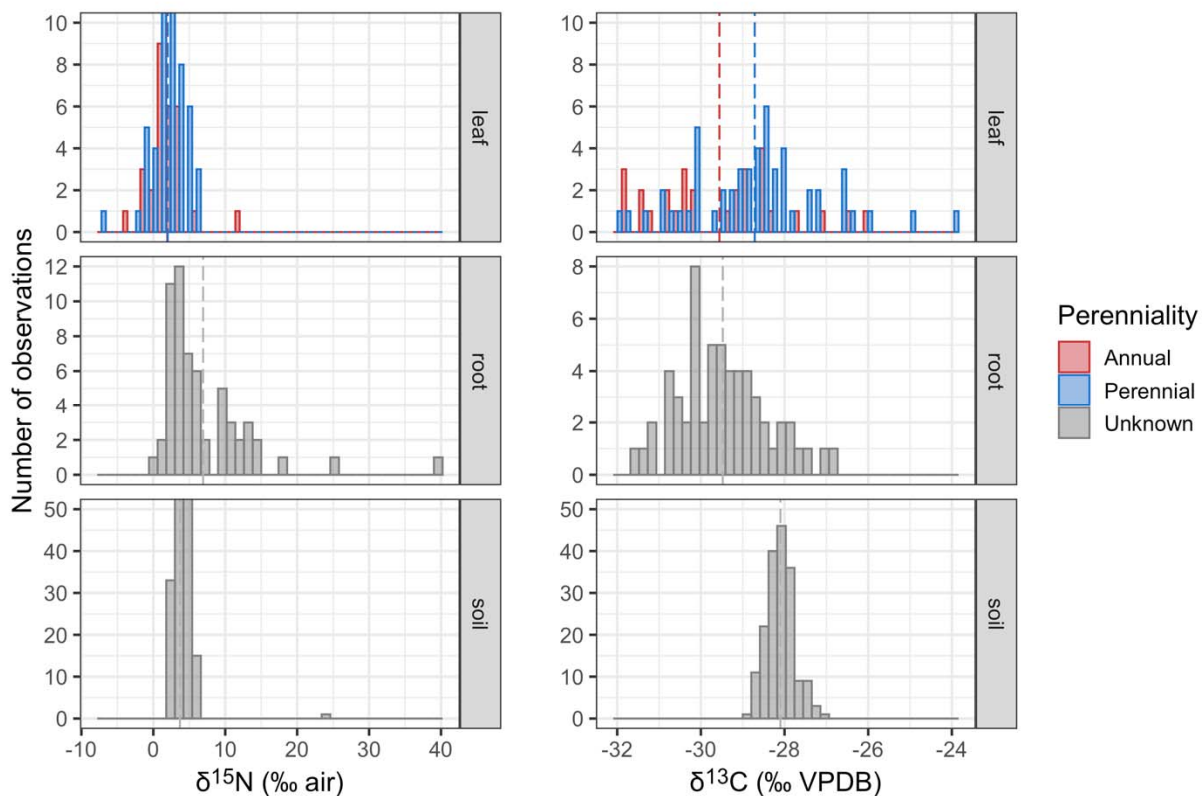
215

216   **Figure 2. Natural abundance of stable isotopes in leaves, roots, and soil before labelling**.

217   Dashed lines indicate mean value.

218

219   To better understand post-labelling soil enrichment, we selected a subset of rhizosphere

220 soils that represented six donor plants at each site divided equally between restored prairie and

221 pasture plots, and selected the three most highly ^{15}N-enriched interspecific receivers in each plot.

222 In addition, we sampled the three most highly enriched interspecific receivers at each site and

223 restored prairie-introduced pasture combination (if they had not been sampled previously).

224 Because pasture plots were sometimes monodominant grasses, we sampled the top three

225 enriched intraspecific receivers at each site and treatment. In total, this came to 48 post-labelling

226 soil samples in 29 plots.

227

228 **Fungal analysis**

229   We extracted DNA from roots of 450 plants harvested at time point 3 (21 days post-label)

230 using Qiagen DNeasy Powersoil HTP kits (Qiagen, Hilden, Germany). We only analyzed DNA

231 from roots, not from the soils collected from each plant's rhizosphere. We characterized each

232 sample's AM fungal composition with a two-step PCR protocol that amplified a ~550bp

233 fragment of the SSU rRNA gene (the most well-supported region for AM fungal taxonomic

234 resolution (Dumbrell et al. 2011)). We used WANDA (5'- CAGCCGCGGTAATTCCAGCT- 3')

235 and AML2 (5'- GAACCCAAACACTTTGGTTTCC-3') primers (Lee et al. 2008, Langmead and

236 Salzberg 2012). We used primers with unique indices so we could multiplex several projects on a

237 single run. We quantified successful PCR amplicons with the Quant-iT PicoGreen dsDNA Assay

238 Kit (Invitrogen, Waltham, MA, USA) on a SpectraMax M5E Microplate Reader (Molecular

239 Devices, San Jose, CA, USA) before purifying with QIAquick PCR Purification kits (Qiagen).

240 We sequenced the purified pools on the Illumina MiSeq platform (paired-end 300bp, Illumina

241 Inc., San Diego, CA, USA) at the University of Oregon Genomics and Cell Characterization

242 Core Facility (Eugene, OR, USA). We used a custom, in-house bioinformatics pipeline to

243 demultiplex reads and filter out duplicate reads generated by PCR duplication using unique

244 molecular identifiers (UMIs) inserted during PCR processing.

245   We assigned amplicon sequence variants (ASVs) using the dada2 pipeline with standard

246 quality filtering and denoising parameters (Callahan et al. 2016). The dada2 pipeline maintains

247 strain-level diversity at the scale of individual sequence variants rather than clustering sequences

248 into OTUs. This fine-scale measure of fungal sequence diversity was particularly important for

249 our analyses to maintain the greatest chance of detecting a single AM fungal 'individual' in

250 multiple plant root samples. Taxonomy was assigned to ASVs using the MaarjAM database

251 (2019 release) (Öpik et al. 2010). We used a Bayesian mixture model in the DESeq2 package

252 (Love et al. 2014) to scale ASV counts within and across samples to avoid artificial taxon

253 abundance biases (Anders and Huber 2010).

254

255 **Data analysis**

256 We performed all analyses in R ver. 4.0.4 (R Core team 2015). We removed one plant

257 with ^{15}N outlier data. We also removed five plants with mislabeled samples. To meet statistical

258 assumptions, we only included data from plants with successful root fungal DNA extraction. In

259 total, we analyzed data from 389 unique plants: 53 donors and 336 receivers.

260 We tested the relationship between NDFL and plant traits and site conditions with a

261 mixed-effect ANOVA (Table 1). We constructed a phyloseq object using the ASV table with

262 normalized counts (McMurdie and Holmes 2013), and used iGraph, metagMisc, and RCy3

263 (Nepusz and Csardi 2006, Mikryukov 2017, Gustavsen et al. 2019) to create networks for each

264 plot. In each network, nodes represented individual plants and edges between nodes represent

265 plants sharing at least one fungal DNA sequence variant. The weighted edges are based on how

266 many fungal ASVs were shared among plants. We calculated degrees of connectivity with

267 tidygraph (Petersen 2022) to examine how many plants each individual plant was 'connected' to

268 (by means of shared fungal ASVs) in each plot (Fig. 3). We also calculated whether each

269 receiver plant shared fungal ASVs with the central donor plant in each plot. We visualized

270 individual plot networks in CytoScape. We visualized shifts in AM fungal community

271 composition using non-metric multi-dimensional scaling (NMDS) in the vegan package,

272 demonstrating the AM fungal community similarity across plants (Oksanen et al. 2022).
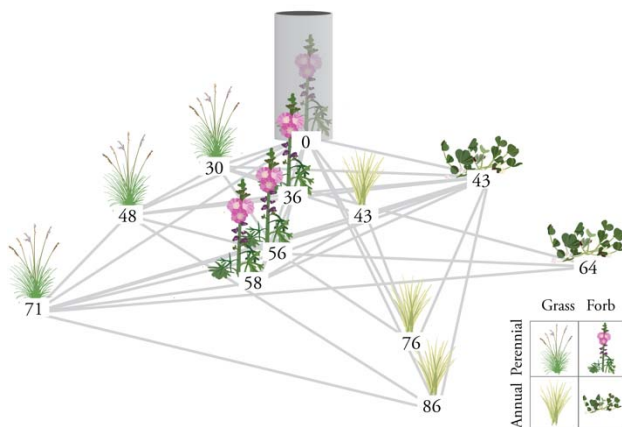

273

274 **Figure 3. Example of how networks were constructed for each plot.** The grey cylinder
275 indicates the donor plant for the plot. Numbers beneath the receivers are the distance (in
276 centimeters) from the donor. Degrees were calculated as how many plants each individual plant
277 was connected to by shared fungal ASVs; for example, the perennial grass at 71 cm has 7
278 degrees.
279
280 **Results**
281   Assimilation of isotopic tracers was similar between labeled "donor" plants with no
282 significant differences on average between sites or experimental treatments within sites,
283 including rainfall exclusion or restored status (Fig. S1). At all sites, foliar assimilation of ^{15}N and
284 ^{13}C by donor plants led to enrichment levels ranging from approximately 5-fold to one order of
285 magnitude higher than baselines, with only a few that were less than 2-fold from baseline. Foliar
286 enrichment levels decreased consistently at all sites and treatments over the 21 day sampling
287 period, suggesting translocation within plants and interspecific transfer between species. We
288 found significant spatial and temporal differences in foliar and root isotope ratios in donors and
289 receivers resulting from interspecific transfer of carbon and nitrogen (Fig. 4; Table 1). Receiver
290 foliar enrichment levels did not correlate with donor foliar enrichment levels within the same
291 plot (Fig. S2).

292
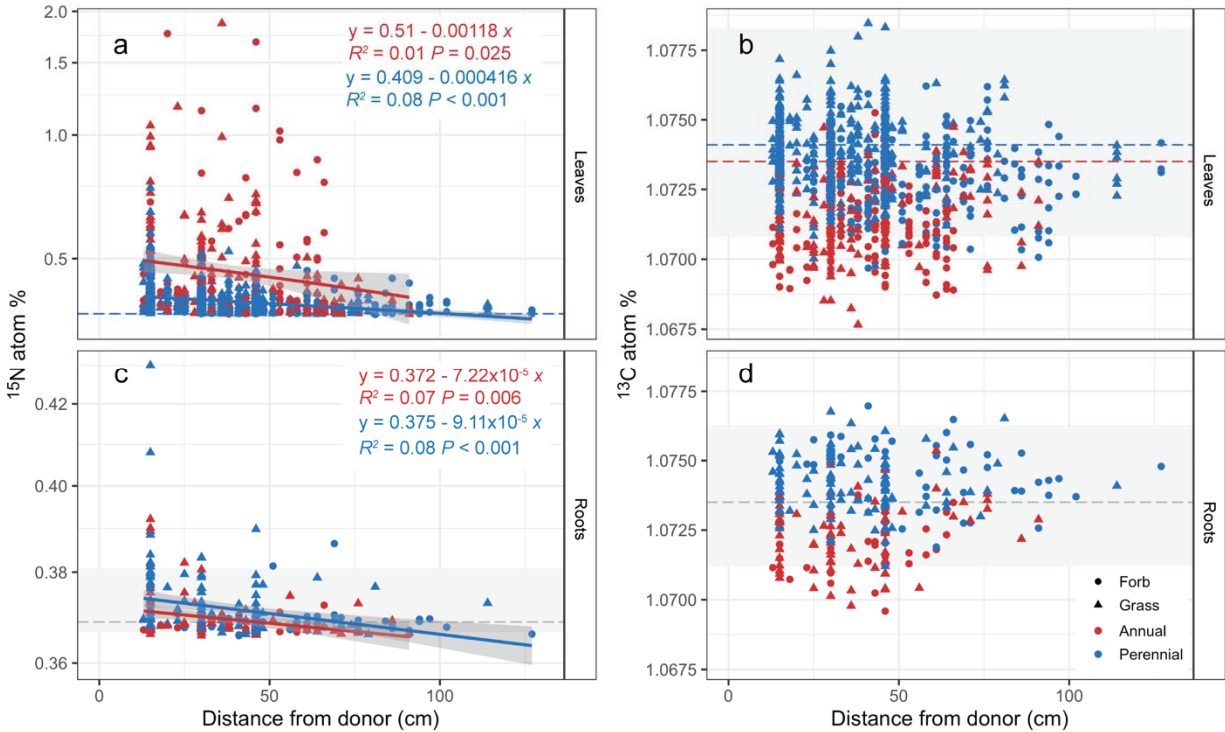
Figure 4. Decreased receiver enrichment with distance from donor in leaves and roots.

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.

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

	χ^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**

300

301   Allocation of ^{13}C and ^{15}N tracers to roots and subsequent transfer to "receiver" species

302 did not follow expected patterns (e.g., despite donors being perennial, annual receivers were

303 more enriched, indicating that relatedness did not drive the transfer, Fig. 4, Table 1) but varied

304 significantly between functional groups due to their intrinsic differences in physiological traits

305 and tissue stoichiometry (Table 1). We selected 18 representative annual/perennial and grass/forb

306 species of receiver plants, which revealed significant differences between functional groups for

307 NDFL (Fig. 5) but no detectable CDFL relative to baseline (Fig. 4).

308   Rain exclusion treatment, restoration treatment, and site did not affect interspecific

309 transfer of nitrogen (Fig S3; ANOVA, P > 0.05, Table 1), and carbon was not enriched enough to

310   test transfer (Fig. 4). We did, however, observe significant differences in nitrogen transfer by

311   functional group (Table 1), mirroring intrinsic differences in tissue stoichiometry and iWUE

312   (Fig. 5), despite no significant enrichment in soils collected from the rhizosphere of those same

313   plants (Fig. S4). C:N affected NDFL (Table 1), but NDFL did not correlate with C:N or iWUE

314   (Fig. 5). We did detect a low level of soil enrichment in 4 out of 23 donor soil samples (ranging

315   from 0.382 to 0.479 atm% ^{15}N).

316   Annuals had greater ^{15}N foliar enrichment compared to perennials (ANOVA, P < 0.001,

317   Tables 1 and 2). Foliar enrichment decreased over both time and space (ANOVA P < 0.001; Fig.

318   4, Fig. S1). On average, annuals had a lower leaf nitrogen content and higher C:N than

319   perennials (Table 2, Fig. 5). Forbs had higher NDFL than grasses (ANOVA, P < 0.001, Table 1)

320   as well as a lower C:N. There was a significant interaction between annual/perennial and

321   grass/forb form (ANOVA, P = 0.003, Table 1).

322

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

324   **labeling**.

			n	*Mean*	±	*SD*	*Min*	*Max*	*Mean*	±	*SD*	*Min*	*Max*
				NDFL					**% N**				
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

325

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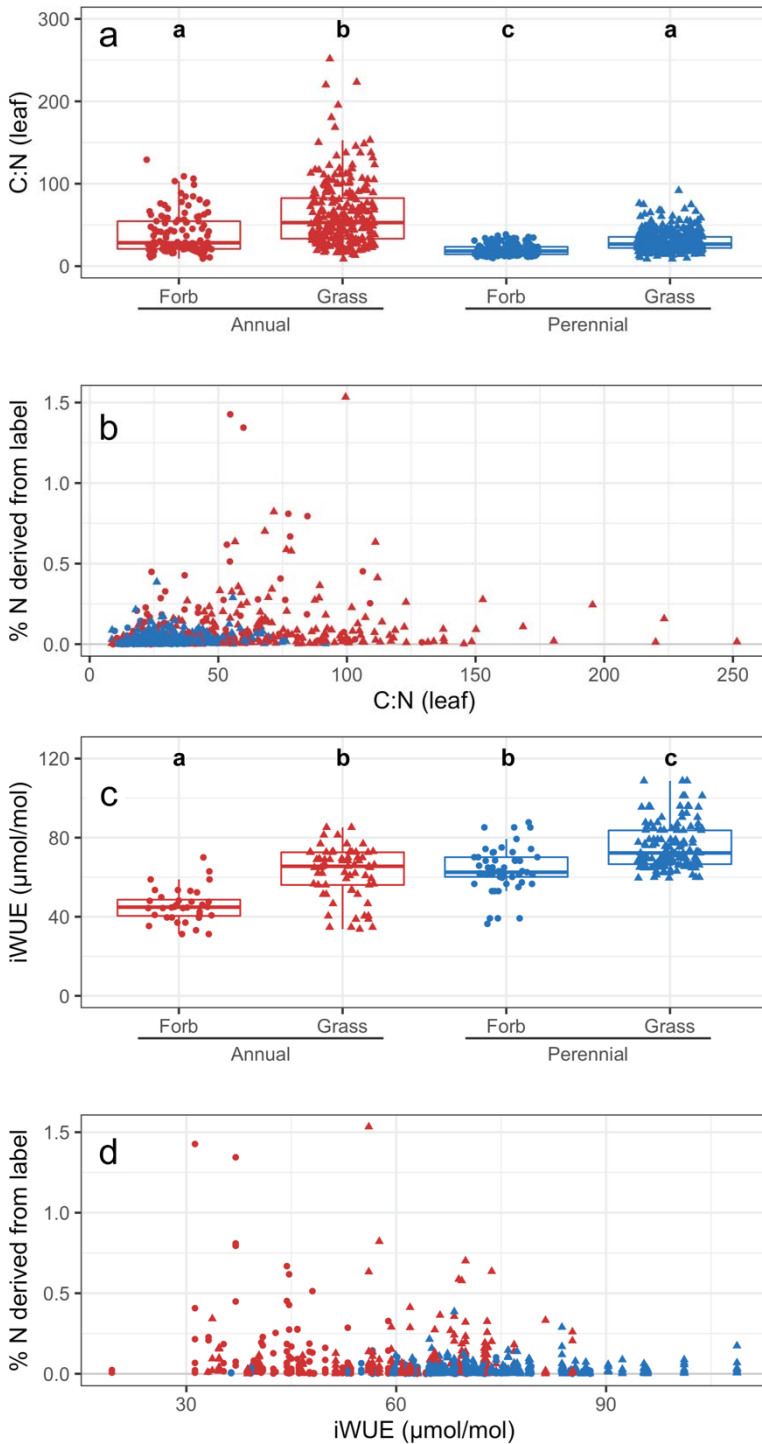
**Figure 5. Stoichiometric and functional traits compared to nitrogen derived from transfer.**

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.

331

332   Our analysis of fungal community composition shows a high degree of connectivity

333 between plants of different species but no obvious pattern of connectedness that could explain

334 preferential nutrient transfer by plant functional groups. Overall, we inferred that plants in all

335 experimental plots and sites were highly 'connected' (as inferred from shared fungal ASVs)

336 because we found that 97.25 % ± 8.01 (SD) of all plants roots within each experimental plot

337 shared at least one fungal DNA sequence variant (ASV) with another plant of the same plot.

338 Fungal community composition was similar across plant functional groups (Fig. 6). Annual

339 plants shared fungi with more plants in the same plot (4.74 plants ± 2.62 SD) compared to

340 perennials (4.04 plants ± 2.49 SD ; t-test, P = 0.019; Table S3), but degrees of connectivity did

341 not predict nitrogen transfer (Table 1). Seventy-three percent of plants were colonized by four or

342 fewer fungi and shared fungi with five or fewer other plants in the plot, making it difficult to

343 determine if strength of connectivity altered nitrogen transfer (Fig. S5).
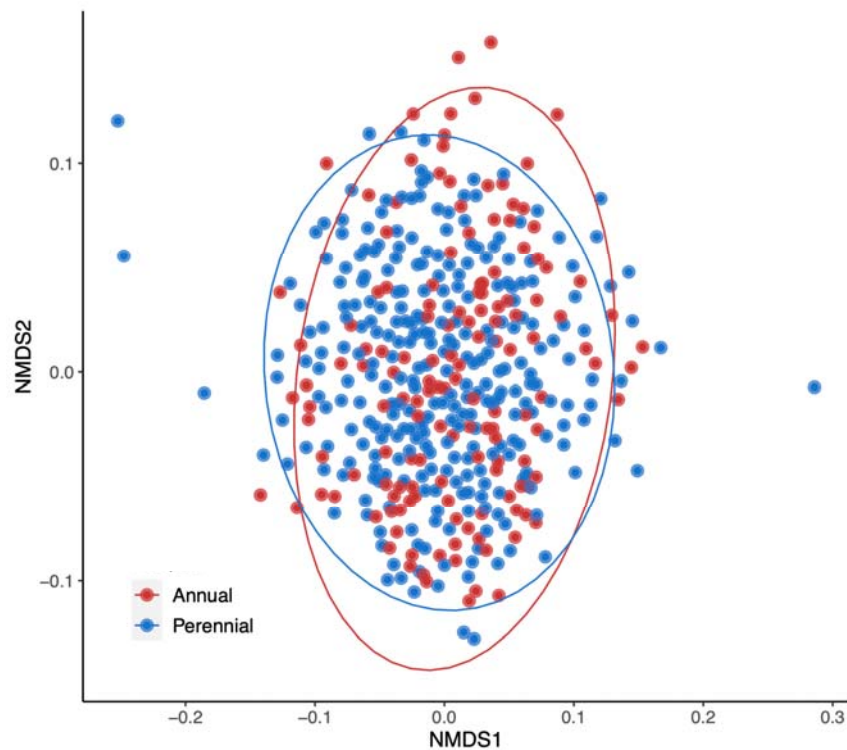
344

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

346 fungal community.

347

348 **Discussion**

349   In our extensively replicated spatiotemporal isotopic tracer experiment, the assimilation
350   and allocation of limiting resources in CMNs was neither plant- nor fungi-centric. Our data show
351   that AM fungi are "agnostic" with respect to plant species composition and relatedness, and that
352   the transfer of nitrogen (the most important nutrient limiting plant growth in our system) is
353   regulated by major functional traits that are known to influence resource use and allocation in
354   plant communities. The rates and direction of resource transfer in CMNs, inferred from pulse
355   labeling and recovery of ^{15}N in leaves and rhizospheres, can be predicted from plant traits and
356   distance from donor species (Fig 1). Across all sites and treatments, we observed a stronger sink
357   for ^{15}N in annual plants close to the source donor, indicating preferential transfer of limiting
358   resources to that functional group of plants. This observation is contrary to the expectation of the
359   kinship hypothesis that preferential transfer would be expected to occur among perennial donors
360   and receivers. Although plants shared a high proportion of fungal ASVs in their roots (Fig. 6),
361   connectivity did not predict ^{15}N transfer (Table 1), and thus we found no evidence for a fungi-
362   centric hypothesis based on which all connected plants would have been expected to be equally
363   enriched in ^{15}N. In summary, our data suggests that the rates and direction of resource transfer in
364   CMNs are ultimately a reflection of plant-fungi interactions manifested in spatiotemporal
365   patterns of resource allocation driven by plant functional traits and sink-source strength
366   gradients.
367   We did not find ^{13}C enrichment in most samples, above- or belowground, and both ^{15}N
368   and ^{13}C signatures of receiver plants were independent of donor or soil enrichment levels. We
369   designed this experiment to be informed by previous hypotheses on how carbon and nitrogen
370   transfer occurs in highly connected CMNs, where a dilution of the applied ^{13}C label is to be
371   expected given the vast amounts of carbon in the soil and plant biomass. We conducted repeated
372   spatiotemporal sampling of isotopic enrichment levels at increasing distances from donor
373   species, days to weeks after labelling, and in well-established communities exposed to multiple
374   years of experimental treatments, expecting to find evidence of kinship (i.e., greatest resource
375   transfer in related plants), driven by CMN economics (i.e., ^{15}N transfer rates coinciding with ^{13}C
376   investment in root and fungal mass). Our donor plants were perennials while annuals received,
377   on average, an order of magnitude higher enrichment. Thus, we discarded kinship as a possible
378   driver of transfer in this system. We also did not find evidence of a relationship between ^{15}N in
379   leaves and ^{13}C in roots. Therefore, here too our data do not support either hypothesis and instead

380   suggest AM fungi are "agnostic" with respect to plant species partnerships, forming CMNs

381   where the rates and direction of resource transfer ultimately reflects a sink-source strength in

382   ecophysiological performance and stoichiometric gradients.

383   Our dual-isotope (^{13}C and ^{15}N) labelling approach was deliberately imposed upon an

384   existing climate experiment to investigate trade between carbon and nitrogen from assimilation

385   to translocation among plant compartments and fungal partners. Our results are consistent with

386   earlier experiments performed in greenhouse experiments under low stress (e.g., temperature

387   controlled and irrigated twice daily) (Silva et al. 2015). However, post-assimilation translocation

388   did not support previous data. Plants acquire CO_2 and NH_3 from the atmosphere and release

389   those same gases into their surroundings, exhibiting a foliar compensation point at which the

390   evolution of gases is equal to assimilation (Farquhar et al. 1980). This compensation point

391   depends on the partial pressure of CO_2 or NH_3 in the mesophyll, and therefore on its partial

392   pressure in the atmosphere, with an increase in leaf uptake expected for both gases as their

393   concentration rises. Our pulse experiment worked for both gases, causing lasting enrichment

394   levels in the leaves of donor species and, over time, in the leaves of receiver individuals of other

395   species, suggesting translocation and transfer (Fig. 4 and S1). This result represents an integrated

396   measure of the total foliar assimilation of NH_3 and CO_2 after a single pulse of isotopically

397   enriched gases.

398   Nitrogen enrichment levels remained high in leaves and many roots at the end of the

399   experiment, allowing us to measure NDFL across the community and infer the main drivers of N

400   transfer. However, carbon enrichment levels faded before plants were harvested approximately

401   21 days post-labelling, either due to losses via respiration or redistribution in CMNs where it

402   became undetectable in all but a few cases. After controlling for variation in assimilation rates,

403   we found that annual plants received greater ^{15}N enrichment than perennial plants. Plants closest

404   to the donor were most enriched, and ^{15}N enrichment decreased over time (Fig. 4). Plant

405   connectivity through a possible CMN did not predict ^{15}N enrichment. We did not detect ^{13}C

406   enrichment in roots, shoots, or soils. Annuals had lower total nitrogen content than perennials,

407   mirroring intrinsic differences in stoichiometry and water-use efficiency (although with no

408   significant correlation found; Fig. 5), indicating that kinship did not drive this transfer as all

409   donor plants were perennials. Although the rainout shelters had limited effect, there were major

410   differences across the latitudinal gradient represented by the sites in temperature and soil

411   moisture availability (some HOPS ref.); however, neither treatment nor site affected our results.

412   The major drivers of differences in allocation of ^{13}C and ^{15}N to roots and subsequent

413   transfer to "receiver" species were the intrinsic difference in physiological traits and tissue

414   stoichiometry between structural groups (annual/perennial or grass/forb; Table 1). This result

415   points to a simple mechanistic explanation to reconcile long-standing questions regarding

416   mutualism and hierarchical transfer of resources between plants via mycorrhizal networks, an

417   explanation that can lead to general predictions of preferential flow of limiting resources in other

418   ecosystems. For example, previous studies in northern California under environmental conditions

419   similar to those found in our southernmost experimental site showed rapid (days to weeks)

420   transfer of ^{15}N applied to the leaves of ectomycorrhizal pines to surrounding annual AM plant

421   receivers (He et al. 2006). Those results were interpreted as evidence for agnostic CMNs because

422   "direct fungal connections are not necessary for N transfer among plants" and "leaves of the

423   annual plants had greater ^{15}N derived from source (NDFS) and were more enriched (^{15}N at %

424   excess and δ^{15}N values) than perennial receivers, irrespective of the mycorrhizal type."

425   Similarly, as proposed by He et al. (2006), our observation of agnostic ^{15}N transfer from donor to

426   receivers suggests that annual plants, with their extensive root systems, were a strong sink for N

427   which could be explained by stoichiometric gradients that affect root exudation and recapture of

428   N-containing materials from rhizodeposition. Our data corroborate rapid agnostic transfer among

429   AM plants, with no detectable enrichment in root or soil ^{13}C near roots 21 days post-labelling,

430   but do not allow us to determine which mechanism is responsible for the ^{15}N transfers.

431   We inferred a high connectivity between plants within each given treatment and site

432   given the highly similar fungal composition in the root systems of both perennial and annual

433   plants (Fig. 6). (Given the constraints of ASV-identified data, we did this analysis on a strain-

434   level scale and we acknowledge there is a chance that separate spores of the same ASV may

435   have separately infected plants within the same plot. However, we are reasonably confident in

436   our use of fungal ASVs as a proxy for connectivity given the strong overlap in our community

437   and because individuals of one ASV can anastomose in the soil (Mikkelsen et al. 2008).) This

438   overlap could explain the lack of support for the kinship hypothesis in our dataset and offers

439   further support for stoichiometric gradients as the fundamental control of terms of trade in

440   CMNs. The marketplace hypothesis proposes that host plants provide the mycorrhizal fungus

441   with carbon in the form of simple sugars. The rate which fungi take up these sugars is controlled

442   by their affinity to the host. Different C sources from a host trigger changes in fungal

443   monosaccharide transporter gene expression, causing fungi to increase N uptake from the soil

444   (Fellbaum et al. 2012). However, host and fungus-specific gene expression differences would be

445   weak in our study sites because our DNA results demonstrate that our plants were highly

446   connected by shared arbuscular mycorrhizal (AM) fungal ASVs. In our case, the ^{15}N we applied

447   to leaves could have mineralized, been recycled at the soil/fungal interface, and converted into

448   basic organic compounds such as amino acids (e.g., via glutamine synthetase or

449   argininosuccinate synthase) which act as charge balance in the catabolic arm of the urea cycle.

450   The fact that we supplied a carbon source (acetate) independent from the C supply of the host

451   could have reduced N transport in the AM symbiosis. Apoplastic transport would then explain

452   how some of the labeled C ended up in plants even though most of it is expected to go to the

453   fungal symbionts. This mechanism also explains how N and mineral elements (e.g., P) are

454   transferred through CMNs from plant to plant even though they are not expected to limit fungal

455   growth (Ward et al. 2022).

456   In conclusion, we found that plant-soil stoichiometric gradients and functional traits were

457   the strongest drivers of resource sharing in grassland CMNs. We interpret this finding as

458   evidence of biochemical and biophysical sinks, in which nutrients are allocated to plants with the

459   greatest need for those nutrients, either through a 'passive' mycorrhizal network or direct uptake

460   from soil, or that nutrients should be allocated through water flow. Expanding on previous

461   studies, we propose that agnostic AM fungi facilitate spatiotemporal dynamics of carbon and

462   nitrogen through CMNs in was that are neither plant- nor fungi-centric. That is, plants and fungi

463   that are located closer together in space and with stronger demand for resources over time are

464   more likely to receive larger amounts of those limiting resources.

465

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474

475   **Data availability statement**

476   Data used in these analyses are available online at the Data Dryad repository

477   (https://doi.org/10.5061/dryad.7pvmcvdxt). While this paper is under review, data can be

478   accessed using the following unpublished link:

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

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