Ecosystems (2006) 9: 305–316
DOI: 10.1007/s10021-005-0110-x

ECOSYSTEMS
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Global Distributions of Arbuscular Mycorrhizal Fungi

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Abstract

We examined potential large-scale controls over the distribution of arbuscular mycorrhizal (AM) fungi and their host plants. Specifically, we tested the hypothesis that AM fungi should be more prevalent in biomes where nutrients are primarily present in mineral, and not organic, forms. Values of percentage root length colonized (%RLC) by AM fungi, AM abundance, and host plant availability were compiled or calculated from published studies to determine biome-level means. Altogether, 151 geographic locations and nine biomes were represented. Percent RLC differed marginally significantly among biomes and was greatest in savannas. AM abundance (defined as total standing root length colonized by AM fungi) varied 63-fold, with lowest values in boreal forests and highest values in temperate grasslands. Biomes did not differ significantly in the percentage of plant species that host AM fungi, averaging 75%. Contrary to the hypothesis, %RLC, AM abundance, and host plant availability were not related to the size, influx, or turnover rate of soil organic matter pools. Instead, AM abundance was positively correlated with standing stocks of fine roots. The global pool of AM biomass within roots might approach 1.4 Pg dry weight. We note that regions harboring the largest stocks of AM fungi are also particularly vulnerable to anthropogenic nitrogen deposition, which could potentially alter global distributions of AM fungi in the near future.

Key words: arbscular mycorrhizal fungi; belowground net primary productivity; fungal biomass; biome; colonization; fine root length; root C:N ratio; soil organic matter; survey.

Introduction

Arbuscular mycorrhizal (AM) fungi are recognized as an important, widespread component of most terrestrial ecosystems. They receive 3–20% of photosynthate from their host plants (Kucey and Paul 1982; Harris and others 1985; Harris and Paul 1987; Jakobsen and Rosendahl 1990; Finlay and Soderstrom 1992; Johnson and others 2002a, b) in exchange for the transfer of soil-derived nutrients to roots, and in this way influence carbon (C) fluxes and nutrient dynamics among plants, soils, and the atmosphere. Moreover, AM fungi are sensitive to various aspects of global change. They often proliferate under elevated atmospheric CO_2 and can also decline under anthropogenic nitrogen (N) deposition (Jansen and Dighton 1990; Diaz 1996; Hodge 1996; Staddon and Fitter 1998; Rillig and others 2002a; Treseder 2004). As such, AM fungi may play a key role in regulating ecosystem responses to environmental change at local to global scales. However, most global change studies of AM fungi are conducted at the ecosystem scale or smaller (Rillig and others 2002a).

To interpret local dynamics of AM fungi within larger scales, we must understand which environmental factors are most important in influencing the global distribution of AM fungi (Allen and others 1995a). Read (1984, 1991a) hypothesized

Received 31 August 2004; accepted 20 January 2005; published online 15 March 2006.
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that the community composition of mycorrhizal fungi would vary as a function of the accumulation of organic matter in the soil. Specifically, AM plants should be more abundant in ecosystems with smaller pools of organic nutrients in the soil, since this group possesses limited ability to degrade organic matter. In contrast, ectomycorrhizal fungi can decompose labile organic nutrients, and their plant hosts should proliferate in areas with moderate organic accumulation. Finally, ericoid mycorrhizal fungi can break down more recalcitrant compounds and should be cultivated in ecosystems with large standing stocks of humified material. In turn, the global distribution of these three mycorrhizal groups could have implications for large-scale fluxes of CO_2 between the soil and the atmosphere (Treseder and Allen 2000). The decomposer activity of ectomycorrhizal fungi and ericoid mycorrhizal fungi should generate a net CO_2 flux from the soil. In contrast, AM fungi can contribute to soil C sequestration by producing glomalin, a recalcitrant and abundant soil glycoprotein (Wright and Upadhyaya 1996; Rillig and others 2001).

What factors other than soil organic nutrients could influence large-scale distributions of AM fungi? Isotope tracers in laboratory and field studies indicate that AM fungi consistently receive 37–47% of C delivered belowground by host plants (Harris and others 1985; Harris and Paul 1987; Jakobsen and Rosendahl 1990; Johnson and others 2002a). Accordingly, AM fungal abundance may simply vary in proportion to belowground net primary productivity (BNPP) of AM plants (Harley 1971). Another possibility is that because fine roots provide a substrate for colonization by AM fungi, fine root length could determine AM biomass.

Finally, mycorrhizal groups may differ in their contributions toward N versus phosphorus (P) uptake by plants. Arbuscular mycorrhizal fungi are thought to play a particularly important role in P acquisition; ectomycorrhizal and ericoid mycorrhizal fungi may be more effective for N (Mosse 1973; Smith and Read 1997). If so, AM abundance may be greater where plants are more limited by P, as indicated by high N:P ratios of plant tissue.

We tested the relative importance of each of these potential regulating factors by compiling published measurements of the percentage of root length colonized (%RLC) by AM fungi and the proportion of plant species that harbor AM fungi in ecosystems representing nine biomes (Appendix, http://www.springerlink.com). In addition, the total length of roots colonized by AM fungi per biome was calculated based on %RLC and others' estimates of fine root stocks (Jackson and others 1997). We quantified differences among biomes in these three parameters, and checked for correlations with pool sizes of soil organic matter (SOM), rates at which organic material is introduced to the soil, and the residence time of SOM. Negative correlations of AM fungi or AM host plants with any of these SOM characteristics would support Read's hypothesis. Positive correlations with either BNPP, fine root length, or plant N:P would indicate that other mechanisms could control AM distribution across biomes.

Methods

For each biome, we estimated three parameters related to AM distributions: %RLC by AM fungi, total standing root length colonized by AM fungi, and the proportion of plant species that host AM fungi. Each index conveys distinct information. In addition, each could potentially—but not necessarily—be controlled by different environmental conditions.

Percentage root length colonized by AM fungi is determined by staining fine roots with dyes targeting AM structures (Koske and Gemma 1989), and then examining stained roots under high (200×) magnification. Generally, 100 or more intersects along the root length are examined for the presence or absence of AM structures (McGonigle and others 1990). The percentage of these intersects that contain AM structures indicates the %RLC by AM fungi. The construction and maintenance of AM structures within the root requires an investment of carbohydrates by the host plant. These resources could otherwise be allocated to root biomass or other plant tissues. It follows that plants with greater %RLC by AM fungi will have allocated a greater portion of their carbohydrates to AM fungi instead of roots (Allen 2001). Percentage root length colonized by AM fungi can therefore be viewed as an indication of the relative investment by plants in AM fungi. This index tends to increase under P limitation of plant growth (Treseder 2004), which is consistent with the notion that plants control allocation of resources to AM fungi based on cost–benefit ratios (Read 1991b; Treseder and Vitousek 2001).

In contrast, the total standing root length colonized by AM fungi should be related to the total biomass of AM fungi in an ecosystem (at least, within plant roots). For example, if two ecosystems display similar levels of %RLC, but different standing stocks of roots, the ecosystem with greater standing root length should have a higher

abundance of AM biomass. The total standing root length colonized by AM fungi is obtained by taking the product of the total standing length of fine roots within each biome, and the average %RLC within each biome. Hereafter, we will refer to total standing root length colonized by AM fungi as ''AM abundance''.

The third parameter that we examined is the proportion of plant species within an ecosystem that can serve as hosts for AM fungi. Most plant species are compatible with AM fungi, with a few notable exceptions (Newman and Reddell 1987). For example, many conifers form relationships with ectomycorrhizal fungi instead of AM fungi. In addition, some grasses are non-mycorrhizal. In ecosystems that are dominated by the latter two groups, the capacity for AM fungi to proliferate may be curtailed owing to lack of potential hosts. The percentage plant species within an ecosystem that can host AM fungi will hereafter be referred to as ''host plant availability''.

We assembled data on %RLC and host plant availability from published field studies representing each biome. We only used data collected from naturally established plants in unmanipulated habitats (for example, no fertilization, planting, weeding, or clearing), although we made exceptions in the case of agricultural systems, where planting, clearing, or weeding were acceptable. No data from fertilized areas were included in the database, even for agricultural studies, because N or P fertilization often influences %RLC (Treseder 2004). Where results were presented in graphs, we estimated values by using digitizing software (Preble 1998). We averaged all data points and sampling times from unmanipulated areas within each location of each study. Locations were assigned to biomes according to geographical setting and the authors' descriptions of study sites.

Altogether, locations ranged from 42°S to 69°N, covering nine biomes in 151 geographical locations (Appendix, http://www.springerlink.com). All continents except Antarctica were represented, although the majority of studies were clustered in North America. The least-represented biomes were desert, savanna, tundra/alpine, and boreal forest, and the most common were temperate grasslands and tropical forests.

Percentage Root Length Colonized

By far, the most common unit of measurement of AM fungal abundance per unit plant biomass is %RLC. Because this technique is used in the majority of field-based AM studies, we were able to assemble directly comparable data from numerous investigators and ecosystems. We classified measurements of %RLC according to sampling approach. In a subset of studies, investigators collected roots from random locations within the ecosystem. We considered the resulting colonization levels to represent the plant community as a whole (that is, ''community-level''). In contrast, the majority of studies focused on particular plant species which were often considered a priori as likely to form relationships with AM fungi (that is, ''species-specific''). We analyzed this group of studies separately, because the %RLC of likely host plants may not necessarily have represented that of the community as a whole.

The calculation of community-level %RLC for cultivated ecosystems was less straightforward than for those of natural ecosystems, because measurements of %RLC in non-AM agricultural systems were very rare. In fact, all the agricultural studies that we compiled were focused on monocultures of AM crop plants. Values of %RLC were therefore assigned to the ''species-specific'' category as well as the ''community-level'' category, because the plant community within a given agricultural ecosystem usually consists of one species. However, we stress that the biome-scale average of community-level %RLC for agricultural areas must be considered an upper bound only. We were not able to incorporate %RLC from non-AM crops, and these would likely reduce our biome-level estimates. As such, we did not include in our statistical analyses the community-level %RLC and AM abundance for this biome.

AM Abundance

By taking the product of root length and mean community-level %RLC for each biome, we acquired an estimate of standing root length colonized by AM fungi. This index is analogous to AM abundance. In most studies in the database, measurements of %RLC were restricted to a subset of roots; typically these were live, fine roots (<2 mm diameter) in the upper 10 cm of soil. Therefore, we estimated root length colonized for only live, fine roots in the top 10 cm of soil. Fine root pools at this depth were derived from Jackson and others (1997, Table 1). Our calculations did not consider AM fungi at lower depths, but %RLC often peaks within the top 15 cm of soil then declines (Figure 1). As such, we expected that our analyses included the majority of AM colonized roots.

Table 1. Arbuscular Mycorrhizal Parameters and Biome-level Characteristics

Biome	Percent RLC, Community-level[a]	Percent RLC, Species-specific[a]	AM Abundance (km colonized root m^{-2})[b]	Host Plant Availability (% plant species)[a]	SOM (kg C m^{-2})[c]	SOM Inputs (kg C m^{-2} y^{-1})[c]	Residence Time of SOM (y)[c]	BNPP (kg C m^{-2} y^{-1})[d]	Live Fine Root length (km m^{-2})[e]	Root N:P[f]	Area (10^{13} m^2)[g]
Boreal Forest	24.5 ± 8.2 (2)	36.3 ± 26.0 (3)	0.28	64.0 ± 31.6 (3)	19.3	0.68	28	0.11	1.15	16.5	1.87
Cultivated	36.3 ± 19.6 (24)[h]	36.3 ± 19.6 (24)	1.50[h]	n.d.				0.05	4.12		2.48
Desert	34.4 (1)	33.2 ± 14.0 (5)	0.36	84.6 ± 22.6 (5)	1.4	0.04	33	0.01	1.05		1.69
Savanna	63.3 ± 0 (2)	43.3 ± 11.5 (5)	9.49	85.5 ± 24.0 (4)	5.4	0.48	11	0.37	15.00	36.3	2.17
Temperate Forest	22.6 ± 3.5 (4)	40.0 ± 31.8 (11)	0.31	56 (1)	12.7	0.91	14	0.21	1.38	10.5	0.99
Temperate Grassland	35.6 ± 18.2 (9)	36.2 ± 21.4 (26)	17.74	80.3 ± 29.2 (8)	13.3	0.30	44	0.18	49.82	7.4	0.90
Tropical Forest	35.8 ± 9.9 (6)	36.0 ± 26.5 (6)	0.31	70.5 ± 27.8 (14)	19.1	3.73	5	0.48	0.87	41.0	1.35
Tundra/Alpine	42.3 (1)	34.4 ± 23.6 (7)	1.92	69.4 ± 39.3 (5)	21.8	0.10	213	0.06	4.53	11.0	0.71
Woodland/Shrubland	34.8 ± 9.7 (3)	31.8 ± 29.0 (13)	1.63	73.7 ± 15.4 (12)	7.6	0.46	16	0.04	4.67		1.10

Percent RLC, percentage root length colonized by arbuscular mycorrhizal fungi; AM, arbuscular mycorrhizal; SOM, soil organic matter; BNPP, belowground net primary productivity; n.d., not determined.
[a]*Mean ± 1 SD (n).*
[b]*Product of mean community-level % root colonization by AM fungi and live fine root length per biome.*
[c]*Data from Amundson (2001).*
[d]*Includes both AM and non-AM plants. Derived from the CASA model (Randerson and others 1997) and compilations of belowground allocation (Saugier and others 2001).*
[e]*Top 10 cm of soil only, including both AM and non-AM plants; calculated from Jackson and others (1997).*
[f]*From Gordon and Jackson (2003).*
[g]*Based on classification schemes developed by Belward and others (1999).*
[h]*Upper-bound of estimate, depending on the proportion of agricultural systems planted with AM host plants.*

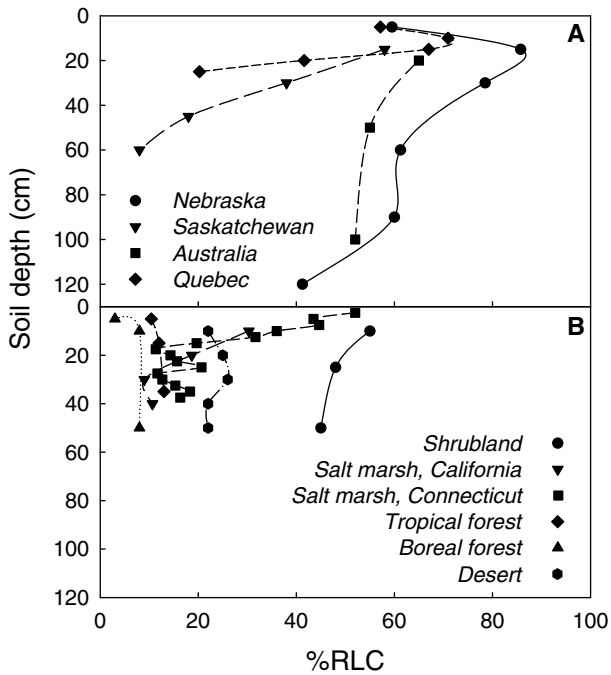

Figure 1. Percent RLC as a function of soil depth, in agricultural (**A**) and natural (**B**) ecosystems. Data are from published field studies (Ellis and others 1992; Cooke and others 1993; Brown and Bledsoe 1996; Germida and Walley 1996; Ingleby and others 1997; Kabir and others 1998; Moyersoen and others 1998; Nehl and others 1999; He and others 2002; Neville and others 2002).

Host Plant Availability

We determined the relative abundance of AM versus non-AM plants in each biome by compiling data from field or nursery studies that had surveyed five or more local plant species for AM colonization (Appendix, http://www.springerlink.com). The percentage of plant species in which AM structures were observed was then averaged across surveys within each biome. All biomes were represented except for agricultural systems. The mycorrhizal status of most crop plants is well established, so surveys of cultivated areas were uncommon. Surveys were likewise rare in temperate forests and boreal forests. Although percent cover, stem density, BNPP, or an analogous measure of relative abundance of AM plants would have been more appropriate for our analyses, these data were not reported often enough to allow for biome-level estimates.

Biome Characteristics

We used data compiled by others to assign values of SOM content, BNPP, live fine root length, and plant nutrients to biomes (Table 1). Pools of SOM (Amundson 2001) signified the amount of nutrients stored in organic form in biomes; SOM inputs (Amundson 2001) indicated the rate at which organic nutrients are made available to mycorrhizal fungi and plants. Residence times of SOM (Amundson 2001) served as an index of recalcitrance of organic nutrients. Live fine root length was calculated for the top 10 cm of soil from Jackson and others (1997). We included root N:P ratios as an indication of the P status of plants relative to N (Gordon and Jackson 2003). Specifically, plants whose growth is limited by P should have higher N:P ratios than would plants limited by N (Koerselman and Meuleman 1996; Aerts and Chapin 2000).

Regional values of NPP were provided by the CASA model (Randerson and others 1997), which uses satellite data of the normalized difference vegetation index (NDVI) and solar insolation to estimate light interception by plant canopies. Net primary productivity was directed belowground according to a biome-level compilation of allocation observations (Saugier and others 2001). Specifically, the percentage of NPP allocated belowground in each biome was: cultivated, 13%; temperate forest, boreal forest, 39%; desert, 40%; tropical forest, 44%; savannas, woodland/shrubland, 50%; tundra/alpine, 57%; and temperate grasslands, 67%. Land regions were assigned to biomes according to the International Geosphere–Biosphere Programme DISCover class scheme, which is based on NDVI (Belward and others 1999).

Statistics

We applied analyses of variance (ANOVA) to test for differences among biomes in AM parameters (SPSS 2000). For species-specific %RLC, AM abundance, and host plant availability, we were unable to transform the data to meet assumptions of the ANOVA. In these cases, ranked data were used. Pearson tests were employed to assess correlations between AM parameters and relevant biome characteristics (SPSS 2000). We considered test results to be significant when P was less than 0.05, and marginally significant when P was less than 0.10.

Results

Percentage Root Length Colonized

Mean %RLC at the community level ranged from 22.6% in temperate forests to 66.3% in savannas

(Table 1), with marginally significant variation among biomes (ANOVA, $F_{7,20} = 2.076$, $P = 0.095$). In contrast, species-specific %RLC did not differ among biomes (ANOVA, $F_{8,91} = 0.120$, $P = 0.998$) and averaged 37.0% overall (Table 1).

AM Abundance

AM fungi were most abundant in temperate grasslands and savannas (Table 1), as a result of high levels of fine root biomass coupled with high %RLC. This value varied widely—63-fold—among biomes. We did not perform statistical tests for differences across biomes, because root length colonized was derived from biome-level means of %RLC and live fine root length.

Host Plant Availability

Generally, 75% of plant species surveyed harbored AM fungi (Table 1), with no significant differences among biomes (ANOVA, $F_{7,44} = 0.733$, $P = 0.645$).

Correlations Between AM Parameters and Biome Characteristics

Soil organic matter pools, inputs, and residence times were often negatively related to %RLC, AM abundance, and host plant availability, but only weakly and non-significantly in most cases (Table 2). The exception was a marginally significant negative correlation between host plant availability and SOM pool size (Table 2). Of the other biome characteristics examined, live fine root length and AM abundance were highly correlated (Figure 2). Marginally significant correlations were observed between BNPP and species-specific %RLC, and between community-level %RLC and host plant availability (Table 2).

Discussion

We found little evidence in support of Read's hypothesis (1984, 1991a) that AM fungi should be less common in ecosystems with greater availability of organic nutrients. Plant allocation to AM fungi (that is, %RLC), AM abundance, and host plant availability did not vary significantly with SOM contents, inputs, or residence times (Table 2), except for a marginally significant negative relationship between host plant availability and SOM content. The extent to which soil nutrients are bound in organic forms did not appear to influence strongly the large-scale distribution of AM fungi.

The best predictor of AM abundance was standing fine root length (Table 2, Figure 2). As such,

Table 2. Pearson Product-moment Coefficients (r), with Sample Sizes in Parentheses

	Percent RLC, Species-Specific	AM Abundance	Host Plant Availability	SOM	SOM Inputs	Residence Time of SOM	BNPP	Live Fine Root Length	Root N:P
Percent RLC, Community-Level	0.424 (8)	0.428 (8)	0.699* (8)	−0.297 (8)	−0.110 (8)	0.123 (8)	0.367 (8)	0.232 (8)	0.521 (6)
Percent RLC, Species-Specific		0.305 (8)	−0.006 (8)	−0.065 (8)	0.080 (8)	−0.276 (8)	0.610* (9)	0.417 (9)	0.365 (6)
AM Abundance			0.511 (8)	−0.139 (8)	−0.269 (8)	−0.037 (8)	0.173 (8)	0.973** (8)	−0.187 (6)
Host Plant Availability				−0.631* (8)	−0.237 (8)	−0.101 (8)	0.036 (8)	0.411 (8)	0.404 (6)

Percent RLC, percentage root length colonized by arbuscular mycorrhizal fungi; AM, arbuscular mycorrhizal; SOM, soil organic matter; BNPP, belowground net primary productivity.
$*P < 0.10$, $**P < 0.0001$.

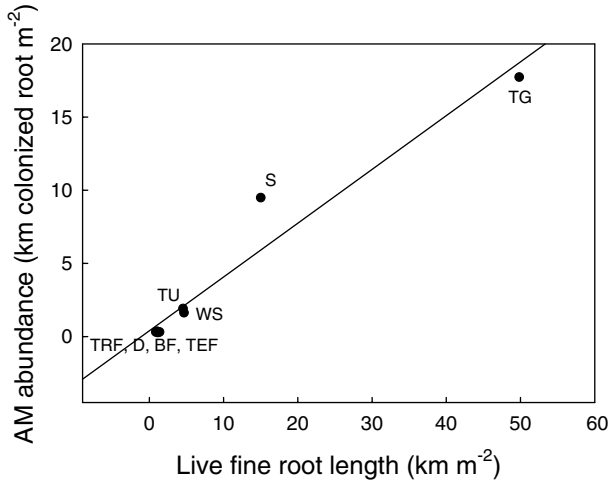

Figure 2. Correlation between AM abundance and fine root length. Each symbol represents one biome. *BF*, boreal forest, *D*, desert, *S*, savanna, *TEF*, temperate forest, *TG*, temperate grassland, *TRF*, tropical forest, *TU*, tundra/alpine, and *WS*, woodland/shrubland. Live fine root length is calculated for the top 10 cm of soil, from Jackson and others (1997).

AM abundance tended to be much greater in grasslands than in other biomes (Table 1). This result may be expected given that fine root lengths were used to calculate AM abundance. However, %RLC was also included in estimates of root length colonized for each biome, yet %RLC was not significantly correlated with root length colonized (Table 2). Apparently, because standing fine root length varied much more widely among biomes than did %RLC (Table 1), standing fine root length wielded stronger influence over AM abundance.

Given that species-specific %RLC did not differ among biomes (Table 1), it appears that AM host plants allocated a fairly consistent proportion of resources to AM fungi (vs. roots) across a broad range of environmental conditions. Likewise, host plant availability did not vary widely (Table 1). Instead, the combination of these two parameters might have elicited differences among biomes in community-level %RLC. Specifically, the product of species-specific %RLC and the proportion of plant species that can host AM fungi should provide a weighted index of allocation to AM fungi on a community basis. This value was significantly correlated with community-level %RLC across biomes ($r = 0.849$, $P < 0.008$). In comparison, species-specific %RLC was not correlated with community-level %RLC when considered independently, and host plant availability was only marginally significantly correlated with community-level %RLC (Table 2). It seems that differences in allocation to AM fungi by plant communities as a whole (that is, community-level %RLC) may have been influenced by the interaction of subtle variations in the host status of plant communities and the degree to which AM fungi are supported by individual host plants. In turn, host plant availability may have been somewhat inhibited by SOM content, and species-specific %RLC may have tended to increase under higher rates of BNPP (Table 2). However, statistical support for these latter two relationships was not strong.

Our results are derived from a compilation of data from diverse studies, each conducted at different dates, with different sampling regimes, and with potentially different protocols. For instance, even though the staining of fine roots for AM colonization is a widespread approach, investigators vary in their choice of stains (that is, Trypan Blue vs. Chlorazol Black E), clearing times, and degree of root bleaching (Koske and Gemma 1989). The quantification of %RLC under magnification is also somewhat subjective, because the investigator must often distinguish between AM and non-AM fungi based on morphological differences. These inconsistencies may have contributed to variation in results among studies, which would limit our statistical power.

How much AM biomass is represented by our estimates of AM abundance? We can roughly approximate intraradical fungal biomass by using the formula $B = \pi \cdot r^2 \cdot L \cdot K \cdot D$, where B is dry biomass; r is root radius, L is root length colonized, K is the fraction of colonized root volume that is fungal, and D is fungal density (Toth and others 1991). The radius of fine roots averages 0.11 mm for grasses, 0.22 mm for shrubs, and 0.58 mm for trees (Jackson and others 1997). Toth and others (1991) have proposed a K value of 0.06, and Van Veen and Paul (1979) estimate fungal density as 1.1 g dry weight cm^{-3}. Accordingly, pools of AM biomass within plant roots could range from 4 g m^{-2} in deserts to 44 g m^{-2} in grasslands. Global totals might approach 1.4 Pg dry weight. This value includes neither extraradical AM hyphae nor intraradical AM structures below 10 cm soil depth. It also does not account for agricultural systems, which likely total 0.05 Pg or less. The accuracy of this estimate is also limited by the accuracy of the value of K, which has only been assessed in a couple of systems (Toth and others 1991). In comparison, direct measurements indicate that total microbial C in soils (including fungi, bacteria, archaea, and protists) reaches 13.9 Pg worldwide (Wardle 1992). Assuming that AM tissues contain approximately 41% C (Paul and Clark 1996), in-

traradical AM fungi could constitute about 4% of the global microbial C pool.

Biomes vary in their susceptibility to global change, with potential consequences for large-scale distributions of AM fungi. Nitrogen additions decrease investment in AM fungi by plants (assessed primarily as %RLC) by an average of 24% in field studies (Treseder 2004). Temperate grasslands of North America and Asia are often exposed to anthropogenic N deposition from neighboring agricultural areas (Galloway and Cowling 2002). These regions harbor relatively large standing stocks of AM fungi (Table 1), so any inhibition of AM growth by N there may become relevant on a global scale. Alternately, if plants in this biome use AM fungi primarily to acquire P, then N effects may be less apparent. To date, AM responses have been determined in only a few N fertilization studies in temperate grasslands, with mixed results (Anderson and Liberta 1992; Bentivenga and Hetrick 1992; Grogan and Chapin 2000; Johnson and others 2003; Treseder 2004). Another consideration is that a doubling of atmospheric CO_2 concentrations consistently produces an increase in AM investment (primarily as %RLC), by an average of 84% (Treseder 2004). This effect could be more widespread, because CO_2 enrichment is a global phenomenon. Finally, production rates of glomalin can be positively related to AM biomass (Wright and Upadhyaya 1996), so that temperate grasslands and savannas may be important targets for assessments of potential C sequestration in glomalin stocks under global change. Our hope is that the information presented here proves useful in examining these and other potential large-scale consequences of environmental change in relation to AM fungi.

ACKNOWLEDGMENTS

We are grateful to L. Marzec, D. Thalp, and A. Reynolds for technical support, and to those investigators whose studies are included in the dataset. This work was funded by grants from the Mellon Foundation, NSF Ecosystems (DEB 010776, DEB 0122445) and the University of Pennsylvania Research Foundation.

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