Final Report

Controls on the production, incorporation and decomposition of glomalin – a novel fungal soil protein important to soil carbon sequestration

PI: **Dr. Matthias C. Rillig**
Division of Biological Sciences
The University of Montana
Missoula, MT 59812

matthias@mso.umt.edu
Tel (406) 243-2389
Fax (406) 243-4184

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This report covers the Montana portion of this project.

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Overview, impact and summary

Glomalin is an operationally defined soil protein, produced by arbuscular mycorrhizal fungi (AMF), with importance in soil carbon sequestration through its relationship with soil aggregation. The goal of the project was to further explore the natural history of glomalin and to address several questions regarding basic behavior of this compound in soil (production, incorporation, decomposition). We have obtained a significant amount of novel information on the arbuscular mycorrhizal fungal soil protein, concerning factors controlling its production to mechanisms of incorporation and decomposition. These findings have resulted in 10 publications in peer-reviewed journals, with several more submitted or in preparation, and 16 contributed presentations at meetings. I have sought collaborative opportunities whenever they fit within the research proposed to enhance our productivity. Additionally, although not part of the original proposed work, we have made a significant effort to elucidate the molecular biology of glomalin (in response to Program Officer suggestions).

In addition to peer-reviewed publications there have also been a number of invited presentations, including a keynote address delivered by the PI at the International Conference on Mycorrhizae (ICOM4) in Montreal, summer 2003. Two Master's students have been trained (and graduated), and a postdoctoral associate has been mentored, as well as numerous undergraduate researchers at UM.

The following sections (A to D) summarize the major findings of the project in the areas of glomalin production control (host factors, elevated CO_2), incorporation, and decomposition. Section D is newly added and describes recent progress in molecular biology. Briefly, we found that glomalin production is influenced by the host, as shown by host species effects and responses to elevated CO_2. We have recently made a significant breakthrough in understanding how glomalin may become deposited into soil; apparently the dominant pathway is via hyphal turnover rather than by secretion (as previously assumed). In terms of decomposition, we have learned that glomalin is surprisingly stable (data from soil incubation experiments and from carbon dating) and has a residence time far greater than the AMF hyphae (on the order of decades, putting at least some glomalin fractions in the slow soil C pool). Finally, our exploratory work on molecular biology of glomalin has yielded some promising preliminary data (including an immunoreactive band that was used to obtain N-terminal amino acid sequence). While the gene has not yet been identified, this strongly suggests that glomalin is a unique compound; - a significant step from an operational definition (based on soil extraction conditions) to biochemical characterization.

A. Glomalin production is influenced by host, fungus and soil factors.

A.1 Fungal control and A.2 Soil control (scaled down from original proposal; instead focus on molecular biology – not in original proposal; see section D.)

?? Rillig MC, Steinberg PD. 2002. Glomalin production by an arbuscular mycorrhizal fungus: a mechanism of habitat modification. **Soil Biology & Biochemistry** 34: 1371-1374.

In this study we **uncover a novel feedback mechanism** between hyphal growth, physical structure of the growing space (simulated by different size glass beads), and glomalin production. This is also the first clear evidence that glomalin production is fungus controlled (not constitutive), and responsive to environmental factors. In large glass beads, simulating aggregated soil, hyphal growth was high, but glomalin production very low. The converse was the case for small glass beads; this suggested that **under non-favorable growing conditions (due to lack of macropore spaces), glomalin production can be increased.** Taken together with the strong correlation of glomalin with soil aggregate stability, this builds a strong case for a feedback mechanism involved in soil aggregation.

A.3 Host control

?? Rillig, M.C., Wright, S.F., Eviner, V.T. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. **Plant and Soil** 238: 325-333.

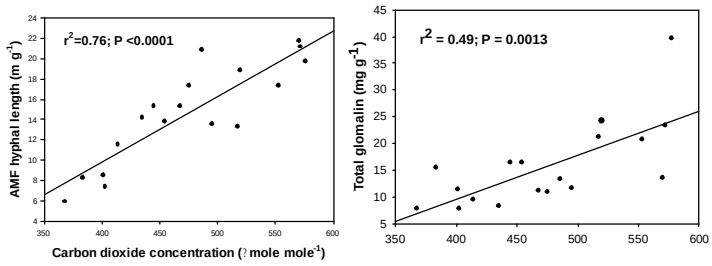
In order to examine the influence of different plant hosts from the same grassland ecosystem on the pools of soil glomalin, we collaborated with V. Eviner (UC Berkeley) on a 2-year field experiment in California. We analyzed soils from monocultures of several different plant species (8 replicates) and found significant differences in the glomalin pools among these plant hosts (immunoreactive EEG: $P<0.05$ [ANOVA]), ranging from 0.81 (standard error: 0.05) mg g^{-1} (*Avena barbata*) to 0.56 (standard error: 0.03) mg g^{-1} (*Amsinckia douglasiana*; fiddleneck). This indicated clearly that **plant species can influence glomalin concentration in soil** from the same ecosystem, highlighting the possibility for a so far unknown link between plant species composition and soil carbon storage. We used **path analysis** to elucidate the relative role of hyphae versus glomalin, concluding that glomalin contributed a far stronger effect to water stability of aggregates than the hyphae producing it.

Plant host effects: elevated atmospheric CO_2

?? Rillig, M.C., Hernandez, G.Y., Newton, P.C.D. 2000. Arbuscular mycorrhizae respond to elevated atmospheric CO2 after long-term exposure: evidence from a CO_2 spring in New Zealand supports the resource-balance model. **Ecology Letters** 3: 475-478.

In an exciting and unique opportunity to confirm the short-term observations with observations on a long-term natural experiment, we collaborated with the research group of Dr. P. Newton (New Zealand), who has identified a CO_2 vent exposing a surrounding grassland to gradients of CO_2 concentrations. Since this vent has been active for at least several decades, our finding of increased percent root colonization, hyphal lengths, and glomalin concentrations along the CO_2 gradient is a confirmation that previously report short-term increases occur over a longer time scales. **This highlights the validity and importance of measuring glomalin as a contributor to soil carbon storage under elevated CO_2.**

Fig. 1: New Zealand CO_2 spring study: along a natural CO_2 gradient, percent fungal root colonization (not shown), hyphal length, and glomalin concentration increase linearly (Rillig et al. 2000).



?? Rillig, M.C., Wright, S.F., Kimball, B.A., Leavitt S.W. 2001. Elevated carbon dioxide and irrigation effects on water stable aggregates in a Sorghum field: a possible role for arbuscular mycorrhizal fungi. **Global Change Biology** 7: 333-337.

In a sorghum [*Sorghum bicolor* (L.) Moench] field experiment in which CO_2 [supplied using free-air CO_2 enrichment (FACE) technology] was crossed factorially with an irrigation treatment, soil aggregate (1-2 mm) water stability increased in response to elevated CO_2. Aggregate water stability was increased by 40% and 20% in response to CO_2, at ample and limited water supply treatments, respectively. Soil hyphal lengths of arbuscular mycorrhizal fungi (AMF) increased strongly in response to CO_2, and the concentrations of one fraction (easily extractable glomalin, EEG) of glomalin were also increased. Two fractions of glomalin, and AMF hyphal lengths were all positively correlated with soil aggregate water stability. Our results support further the hypothesis that AMF can become important in global change scenarios via their effects on soil structure. **This result should be of great importance in agricultural systems, particularly those threatened by erosional soil loss; a positive feedback on soil carbon storage can be postulated.**

Combined host, fungus and soil effects: ecosystem warming (added to original proposal)

?? Rillig MC, Wright SF, Shaw MR, Field CB. 2002. Artificial climate-warming positively affects arbuscular mycorrhizae but decreases soil aggregate water stability in an annual grassland. **Oikos** 97: 52-58.

Despite the importance of arbuscular mycorrhizae to the functioning of terrestrial ecosystems (e.g., nutrient uptake, soil aggregation), and the increasing evidence of global warming, responses of arbuscular mycorrhizal fungi (AMF) to climate-warming are poorly understood. In a field experiment using infrared heaters, we found effects of warming on AMF after one growing season in an annual grassland, in the absence of any effects on measured root parameters (weight, length, average diameter). AMF soil hyphal length was increased by over 40% in the warmed plots, accompanied by a strong trend for AMF root colonization increase. The main result of the study was that the **concentration of glomalin was decreased in the warmed plots, possibly suggesting an increased rate of decomposition of this protein.** Soil aggregate water stability, measured for five diameter size classes, was also decreased significantly. These results indicate that ecosystem warming may have stimulated carbon allocation to AMF, but that other factors (e.g. decomposition) were important in determining the role of these symbionts in soil aggregation. These changes in soil aggregation, if widespread among terrestrial ecosystems, could have important consequences for soil carbon storage and erosion in a warmed climate.

B. Incorporation

The question of how glomalin is incorporated into the soil medium is a very difficult one to address, given our lack of knowledge about cell biology, molecular biology or biochemistry of this compound. However, we have recently made significant progress towards understanding a critical step of this progress, namely the release into soil, using in vitro cultures of an AMF. This resulted from a collaboration with Dr. Holben, a molecular biologist at UM.

?? Driver, J., Holben W.E., Rillig, M.C. Delivery pathway of glomalin into soil: glomalin as a hyphal wall component of the arbuscular mycorrhizal fungus *Glomus intraradices.* Soil Biology & Biochemistry (submitted)

That AMF deposit apparently large amounts of a proteinaceous substance (glomalin) into soil presents a conundrum; AMF, as obligate biotrophs, cannot directly recapture this organic carbon and nitrogen, unlike saprobic soil microbes. This conundrum could potentially be resolved if more were understood concerning the pathway of delivery of glomalin into soil. **Two possible pathways for deposition of glomalin into soil** by AMF mycelium have very different implications for functionality: secretion into the growth medium or environment, or incorporation into the hyphal wall and subsequent release

from this structural component. In this study we tried to distinguish between these two pathways by comparing glomalin accumulation in the culture medium of *in vitro* grown AMF with the amount of glomalin contained in the actual mycelium. We showed that glomalin is significantly more abundant as a mycelium component, compared to a soluble protein in the culture supernatant (Fig. 2), **suggesting that it is not primarily secreted, but released from hyphae subsequently**. In fact, glomalin seems to be extremely tightly (likely covalently bound in the hyphal wall, as extraction conditions necessary for glomalin from mycelium demonstrate (Table 1).

Table 1. Extraction of soluble proteins (quantified by Bradford or BCA assays) and immunoreactive protein (glomalin; ELISA assay using MAb32B11) from *G. intraradices* mycelium using various methods.

Extraction Method	Protein	Immunoreactivity
SDS (2% or 4%) w or w/o DTT	+	-
Sodium citrate 4^{o} C or 37^{o} C	+	-
Urea, 8M with 4% Triton X 100	+	-
2% Acetonitrile pH 8.0	+	-
2% Acetonitrile/0.1% Trifluoroacetic acid	-	-
0.1M NaOH	+	-
1M NaOH	+	-
2M NaOH	+	-
100% Trifluoroacetic acid	+	-
Tris (10 mM)/EDTA (1 mM) pH 8.0, autoclaved	-	-
Guanidine HCl, 4M pH 5.7	+	+
Sodium citrate, autoclaved	+	+

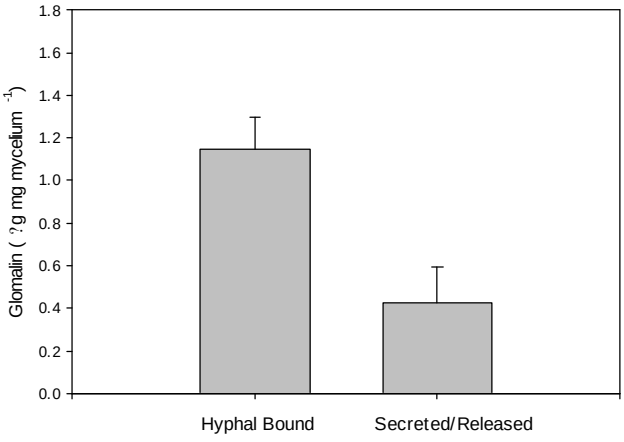


Fig. 2 Relative abundance of glomalin in mycelium (hyphal bound) or in the culture medium (secreted/ released). Differences are significant at $P < 0.001$. This suggests that glomalin arrives in soil primarily via release from decomposing hyphae (see also Table 1). Driver et al. (submitted).

C. Decomposition and turnover

C.1. Decomposition studies

?? Rillig MC, Ramsey PW, Morris S, Paul EA. 2003. Glomalin, an arbuscular-mycorrhizal fungal soil protein, responds to land-use change. **Plant and Soil** 253: 293-299.

In collaboration with Dr. S. Morris and others, we measured glomalin levels and decomposition after a **>400 d incubation in three soils** from a native mixed hardwood forest, an agricultural soil, and an afforested area (1940s) on the same soil type in Ohio. We found the highest glomalin levels in the native forest, followed by the afforested sites, with agricultural soils having much lower glomalin levels. Incubation for >1 year resulted in a significant decrease in glomalin pools in the three different soil types. This indicates a native microbial community is decomposing glomalin, and that the **decomposition is exceptionally slow, placing some glomalin in the slow to recalcitrant C pool** (see Table 2). Some glomalin is quickly respired, however. Additionally, we have provided evidence that glomalin-associated carbon storage is very strongly related with forest practices and secondary succession.

Table 2: Organic C†, CO_2 respired after incubation, % C remaining, EEG and TG, and percentage of glomalin pools remaining after incubation for A, B and C horizon of the three land-use types (standard errors of the mean in brackets). Means followed by a different letter differ significantly (Tukey-Kramer HSD; $P < 0.05$) among land-use types within a horizon. EEG = easily extractable glomalin; TG = total glomalin. From Rillig et al. (2002).

		Organic C (mg/cm^3 soil)	CO_2-C respired (mg/cm^3 soil)	C remaining (%)	EEG (mg/cm^3 soil)	EEG remaining (%)	TG (mg/cm^3 soil)	TG remaining (%)
Aff	A	20.56 (1.85)[a]	2.06 (0.10)[b]	89.80 (0.45)[a]	0.44 (0.02)[a]	36.33 (4.34)[a]	3.41 (0.39)[a]	31.58 (5.77)[b]
Agric	A	17.87 (0.42)[a]	1.31 (0.15)[a]	92.68 (0.89)[b]	0.44 (0.03)[a]	22.82 (0.89)[b]	3.06 (0.13)[a]	46.58 (4.18)[a]
Nat	A	38.52 (1.02)[b]	2.80 (0.09)[c]	92.69 (0.42)[b]	0.46 (0.03)[a]	35.47 (3.50)[a]	4.91 (0.10)[b]	51.84 (1.89)[a]
Aff	B	9.23 (0.65)[a]	0.60 (0.08)[b]	93.74 (1.01)[a]	0.33 (0.01)[a]	39.84 (4.33)[a]	2.01 (0.25)[a]	18.56 (3.43)[a]
Agric	B	8.72 (0.53)[a]	0.30 (0.05)[a]	96.60 (0.40)[b]	0.31 (0.02)[a]	37.38 (1.39)[a]	1.90 (0.27)[a]	31.83 (7.62)[a]
Nat	B	14.47 (0.78)[b]	0.98 (0.67)[c]	93.13 (0.57)[a]	0.42 (0.02)[b]	42.64 (1.52)[a]	2.90 (0.27)[b]	33.07 (4.51)[a]
Aff	C	9.46 (0.47)[a]	0.36 (0.21)[a]	96.09 (0.38)[a]	0.20 (0.01)[a]	48.64 (6.10)[a]	1.08 (0.06)[a]	24.25 (6.32)[a]
Agric	C	9.42 (0.36)[a]	0.21 (0.16)[a]	96.67 (0.63)[a]	0.19 (0.03)[a]	12.44 (0.55)[b]	1.18 (0.10)[a]	22.88 (18.79)[a]
Nat	C	11.39 (0.58)[b]	0.44 (0.92)[a]	95.19 (0.40)[a]	0.21 (0.01)[a]	23.89 (5.32)[c]	1.23 (0.07)[a]	21.95 (7.67)[a]

?? Steinberg PD, Rillig MC. 2003. Differential decomposition of arbuscular mycorrhizal fungal hyphae and glomalin**. Soil Biology & Biochemistry** 35: 191-194.

In this study we show directly that glomalin turns over considerably slower in soils than the hyphae that produce it. We used an experimental design that exploited the lack of saprobic capabilities of AMF hyphae by incubating field soil samples in the dark, and hence in the absence of plant or AMF hyphal growth. In 150 days, hyphal length decreased 60%, while glomalin, quantified by the Bradford protein assay, declined only 25%. Immuno-reactive total glomalin decreased 46%. Importantly, in this study we also were able to show that one glomalin pool, **IREEG (immunoreactive easily extractable glomalin; the fraction generally most strongly correlated with aggregate stability) actually increased during decomposition** (Fig. 3). This indicates that IREEG is not composed only, as hypothesized, of the most recently produced glomalin, but also represents recently mobilized glomalin. This study also serves as a proof-of-concept for decomposition of hyphae and glomalin that could be used to study influence of a variety of soil factors.

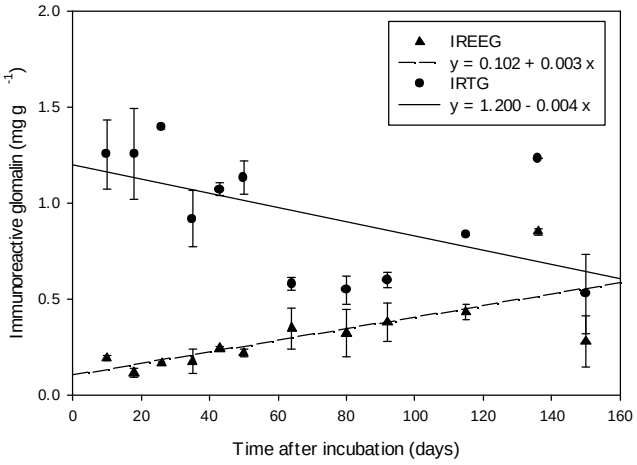


Fig. 3 Changes in immunoreactive glomalin pools through a decomposition time series. The IREEG pool actually increases over the time period, while the total amount of immunoreactive glomalin (IRTG; which includes IREEG) decreases, as expected. From Steinberg and Rillig (2003).

?? Lutgen ER, Clairmont DL, Graham J, Rillig MC. 2003. Seasonality of arbuscular mycorrhizal hyphae and glomalin in a western Montana grassland. **Plant and Soil** (in press)

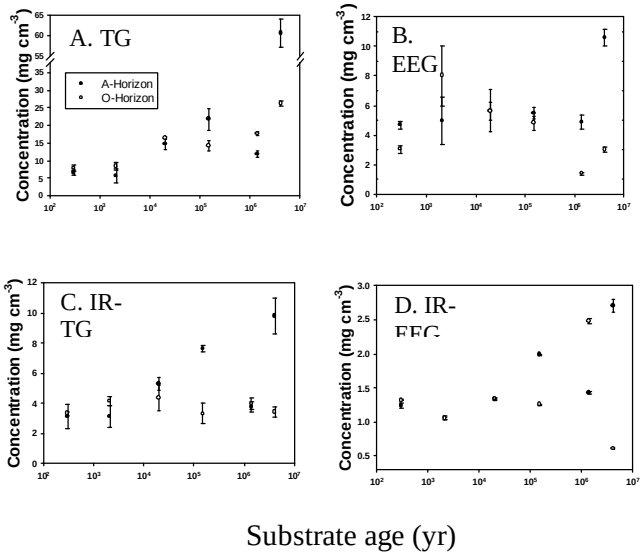
If glomalin is relatively stable in soils, we would expect comparatively small seasonal changes in glomalin pools. To test this hypothesis we measured glomalin pools repeatedly throughout a growing season in Montana grassland. **We found that glomalin has a much lower coefficient of variation throughout the season compared to other AMF parameters,** such as hyphal lengths and root colonization. This study was the first examination of seasonal patterns of glomalin, and this is important information for study design.

C.2. Glomalin across a tropical chronosequence; carbon dating

?? Rillig, M.C., Wright, S.F., Nichols, K.A., Schmidt, W.F., Torn, M.S. 2001. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. **Plant and Soil** 233: 167-177.

Glomalin was detected in tropical soils in concentrations of over 60 mg cm^{-3}. Along a chronosequence of soils spanning ages from 300 yr to 4.1 Mio yr, a pattern of glomalin concentrations is consistent with the hypothesis that this protein accumulates in soil (Fig. 4). **Carbon dating of glomalin indicated turnover at time scales of several years to decades**, much longer than the turnover of AMF hyphae (which is assumed to be on the order of days to weeks). This suggests that contributions of mycorrhizae to soil carbon storage based on hyphal biomass in soil and roots may be an underestimate. **The amount of C and N in glomalin represented a sizeable amount (ca. 4 to 5%) of total soil C and N** in the oldest soils. Our results thus indicate that microbial (fungal) carbon that is not derived from above- or below-ground litter can make a significant contribution to soil carbon and nitrogen pools, and can far exceed the contributions of soil microbial biomass (ranging from 0.08 to 0.2% of total C for the oldest soils).

Fig. 4 Pattern of the 4 different glomalin pools across a tropical chronosequence. Data are separated by horizon (O and A). From Rillig et al. (2001).



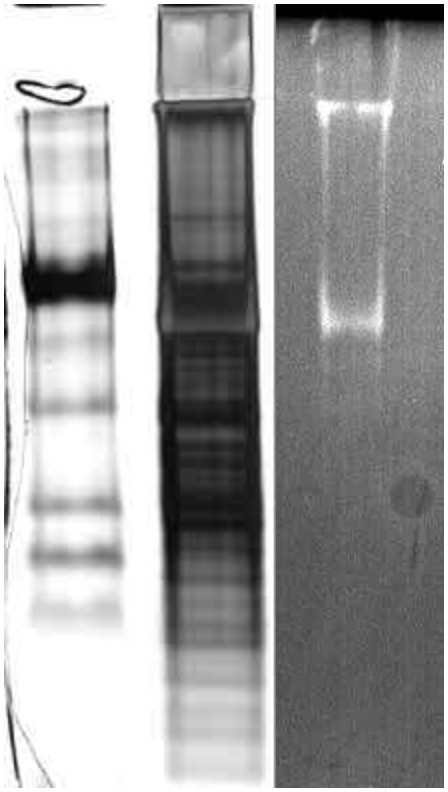
C.3. Degradation of glomalin by soil microorganisms (**cut from proposal; only funded for 2 years**)

D. Exploring molecular biology of glomalin **(added to the original proposal)**

?? Driver, J., Rillig, M.C. Glomalin, and arbuscular mycorrhizal fungal soil protein, as a unique compound. Applied and Environmental Microbiology (in prep.)

Glomalin is an operationally defined compound, and there is little biochemical information available. Efforts at elucidating aspects of the biochemistry or molecular biology of glomalin have been hampered by attempting to work with soil-derived material (this turns out to be a dead end). We moved to working with *in vitro* culture material and have made significant progress: **for the first time, we were able to blot a band that was immunoreactive (Fig. 5). From this band we obtained N-terminal protein sequence.** We have designed several degenerate primer pairs to that sequence, and we have probed a cDNA library from *G. intraradices* we constructed. This work is ongoing with additional funding, but so far we have not been able to identify a gene.

Fig. 5 Lanes from left to right: MW ladder, extract of proteins from AMF hyphae grown in vitro culture, immunoblot with MAb32B11. There is clearly a strong immunoreactive band, in addition to material still retained in the loading area of the gel (reminiscent of hydrophobin gels).



Peer-reviewed publications (10, ordered chronologically)

?? Rillig, M.C., Hernandez, G.Y.*****, Newton, P.C.D. 2000. Arbuscular mycorrhizae respond to elevated atmospheric CO2 after long-term exposure: evidence from a CO2 spring in New Zealand supports the resource-balance model. **Ecology Letters** 3: 475-478.

?? Rillig, M.C., Wright, S.F., Nichols, K.A., Schmidt, W.F., Torn, M.S. 2001. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. **Plant and Soil** 233: 167-177.

?? Rillig, M.C., Wright, S.F., Kimball, B.A., Leavitt S.W. 2001. Elevated carbon dioxide and irrigation effects on water stable aggregates in a Sorghum field: a possible role for arbuscular mycorrhizal fungi. **Global Change Biology** 7: 333-337.

?? Rillig MC, Steinberg PD. 2002. Glomalin production by an arbuscular mycorrhizal fungus: a mechanism of habitat modification. **Soil Biology & Biochemistry** 34: 1371-1374.

?? Rillig, M.C., Wright, S.F., Eviner, V.T. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. **Plant and Soil** 238: 325-333.

?? Rillig MC, Wright SF, Shaw MR, Field CB. 2002. Artificial climate-warming positively affects arbuscular mycorrhizae but decreases soil aggregate water stability in an annual grassland. **Oikos** 97: 52-58.

?? Lutgen ER, Clairmont DL[#], Graham J, Rillig MC. 2003. Seasonality of arbuscular mycorrhizal hyphae and glomalin in a western Montana grassland. **Plant and Soil** (in press)

?? Rillig, MC, Maestre FT, Lamit LJ. 2003. Microsite differences in fungal hyphal length, glomalin, and soil aggregate stability in semiarid Mediterranean steppes. **Soil Biology & Biochemistry** 35: 1257-1260.

?? Rillig MC, Ramsey PW, Morris S, Paul EA. 2003. Glomalin, an arbuscular-mycorrhizal fungal soil protein, responds to land-use change. **Plant and Soil** 253: 293-299.

?? Steinberg PD, Rillig MC. 2003. Differential decomposition of arbuscular mycorrhizal fungal hyphae and glomalin**. Soil Biology & Biochemistry** 35: 191-194.

Other refereed publications

?? Rillig MC, Treseder KK, Allen MF 2002 Global change and mycorrhizal fungi. In: van der Heijden MGA, Sanders I (eds), **Mycorrhizal Ecology**. Ecological Studies 157, Springer Verlag, Berlin, pp 135-160.

Manuscripts in preparation or submitted

?? Driver, J., Holben W.E., Rillig, M.C. Delivery pathway of glomalin into soil: glomalin as a hyphal wall component of the arbuscular mycorrhizal fungus *Glomus intraradices.* Soil Biology & Biochemistry (submitted)

?? Driver, J., Rillig, M.C. Glomalin, and arbuscular mycorrhizal fungal soil protein, as a unique compound. Applied and Environmental Microbiology (in prep.)

Papers and posters presented at national or international meetings (16, ordered chronologically)

?? Glomalin, the scum of the earth. Rillig MC. Montana EPSCoR "Environmental Science" meeting, Lubrecht Experiment Forest, MT, 1999

?? Glomalin and increased water stability of soil aggregates under global change. Rillig MC. Society for Conservation Biology, Missoula, MT, June 2000.

?? Production of the arbuscular mycorrhizal fungal protein glomalin: the role of host plant species. Rillig MC, Wright SF, Eviner V. Ecological Society of America Annual Meeting, Snowbird, UT, August 2000.

?? The effects of global change on belowground carbon storage: Under elevated CO_2, increased N-deposition does not lead to increased C storage in a California grassland. Shaw MR, Torn MS, Field CB, Rillig MC, Mooney HA. Ecological Society of America Annual Meeting, Snowbird, UT, August 2000.

?? An arbuscular mycorrhizal fungus responds to its physical growing space by altered growth and glomalin production. Rillig MC, Steinberg PD. The Soil Ecology Society Conference, Pine Mountain, Georgia, May 2001 (p. 24).

?? Belowground and simulated aboveground herbivory decrease the production of the arbuscular mycorrhizal fungal protein glomalin. Hernandez, GY, Wilson GWT, Hartnett DC, Rillig MC. The Soil Ecology Society Conference, Pine Mountain, Georgia, May 2001 (p. 42).

?? Decomposition of arbuscular mycorrhizal fungal hyphae and glomalin. Steinberg PD, Rillig MC. The Soil Ecology Society Conference, Pine Mountain, Georgia, May 2001 (p. 56).

?? Production of the protein glomalin by arbuscular mycorrhizal fungi: a mechanism of habitat modification? Rillig, M.C. ISME-9 Interactions in the Microbial World, Amsterdam, The Netherlands, p. 267.

?? Rillig MC, Klironomos JN. 2002. The arbuscular mycorrhzial fungal soil protein glomalin influences hyphal palatability. Ecological Society of America Annual Meeting, Tucson, p. 415

?? Niklaus PA, Newton PCD, Rillig MC. 2002. Soil moisture feedback to elevated CO2 via alterations of soil physico-chemical structure. GCTE workshop, Basel, Switzerland.

?? Rillig MC. 2002. The arbuscular mycorrhizal fungal soil protein glomalin: understanding its role in fungal biology. New Zealand Soil Science Society Golden Jubilee Conference, Wellington, New Zealand

?? Rillig MC, Lutgen ER, Ramsey PR, Muir-Clairmont D, Lamit LJ and Morris SJ. 2003. The arbuscular mycorrhizal fungal protein glomalin: spatial and temporal patterns. Soil Ecology Society International Conference, Palm Springs, CA.

?? Rillig MC, Lutgen ER, Rosier C. 2003. The role of different arbuscular mycorrhizal fungi in soil aggregation. Ecological Society of America Annual Meeting, Savannah, Georgia.

?? Driver JD, Rillig MC. 2003. The secreted AM fungal protein glomalin binds strontium in solution. International Conference on Mycorrhizae ICOM4, Montréal Canada, p.225.

?? Driver JD, Rillig MC. 2003. The arbuscular mycorrhizal fungal soil protein glomalin, a distinct compound. International Conference on Mycorrhizae ICOM4, Montréal Canada, p.226.

?? Lutgen ER, Muir-Clairmont D, Graham J, Krivtsov V, Deyo N, Rillig MC. 2003. Seasonality of the arbuscular mycorrhizal fungal soil protein glomalin. International Conference on Mycorrhizae ICOM4, Montréal Canada, p.228.