Mycorrhiza (2003) 13:205–210
DOI 10.1007/s00572-002-0218-1

ORIGINAL PAPER

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Glomalin content of forest soils in relation to fire frequency and landscape position

Received: 26 June 2002 / Accepted: 26 November 2002 / Published online: 6 February 2003

Abstract Low-intensity, dormant season fires were frequent and widespread in oak-hickory (*Quercus-Carya*) forests of eastern North America until widespread fire suppression began in the mid-1900s. To assess how reintroduction of fire into such ecosystems might affect the activity of arbuscular mycorrhizal (AM) fungi and, thereby, predict the long-term responses of plants and soils to fire, we analyzed the content of the immunoreactive fractions of the AM-fungus-specific glycoprotein glomalin in soils taken in 1994 and 2000 from three forested watersheds in southern Ohio, USA. One watershed remained unburned, one was burned annually from 1996–1999 and one was burned twice, in 1996 and 1999. In addition, to account for the strong landscape-scale gradients of microclimate and soil that typify these watersheds, we stratified each watershed-scale treatment area into three microclimatic zones (=landscape positions) using a GIS-based integrated moisture index (IMI). In the unburned control, the concentrations of immunoreactive, easily-extractable glomalin (IREEG) and immunoreactive total glomalin (IRTG) did not change significantly over the 6-year interval between sampling times, either overall or within any of the three IMI classes. IRTG content was greatest in the mesic landscape positions and lowest in the relatively xeric landscape positions, but IREEG did not vary among landscape positions. Neither IREEG nor IRTG contents were affected by fire, nor were there significant interactions between fire and landscape position in glomalin content. Both correlation and regression analyses demonstrated significant linkages between soil glomalin content, the density/diversity of herbaceous plants, and soil N availability. Despite significant effects of fires on soil N availability and root growth, we resolved no effect of fire on AM fungal activity at this spatial scale.

Keywords Glomalin · AM fungi · Oak-hickory · *Quercus-Carya* · Forest · Fire

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Introduction

In regions where frequent, low-intensity, dormant season fires were once common, such as the oak-hickory (*Quercus-Carya*) forest region of eastern North America, widespread suppression of fire since the 1930s has led to large accumulations of litter, humus, and coarse woody debris. In addition, the suppression of fire appears to correlate closely with ongoing changes in woody plant species composition and community structure in these forests (Iverson et al. 1997). In recognition of these changes, prescribed fire has become an increasingly important tool for ecosystem management in such regions (Cooper 1971; Riebold 1971; Sutherland and Hutchinson 2003).

Prescribed fire can affect plant community diversity and community structure through direct, fire-induced mortality, through modification of the microclimate near ground level, and through changes in chemical, biochemical, and microbial characteristics of the forest floor and mineral soil (Boerner 2000). Although considerable research has focused on both the changes in plant communities and soil chemical properties following fire in this region, little effort has been made to date to link below-ground chemical and biological effects with changes in the plant community in a mechanistic, causal fashion (Boerner 2000). For example, changes in plant density and species composition might be expected to result in changes in the abundance and activity of mycorrhizal fungi that depend on those plants. At the same time, changes in soil chemistry and forest floor

microclimate might affect the growth and activity of various species or groups of mycorrhizal fungi directly, with such changes causing subsequent effects on performance of specific plant species and eventually on plant community structure. Thus, plants, mycorrhizal fungi, and soil chemical and physical factors that vary across the landscape and with fire are likely to be interlinked in ecologically important networks. The general goal of this study may be seen as a first step towards elucidating such interactions.

In 1994, we began a series of experiments designed to assess the effect of reintroducing dormant season, low-intensity fire in oak-hickory forests of southern Ohio (Sutherland and Hutchinson 2003). In the study presented, we focused specifically on how prescribed fire affects arbuscular mycorrhizae (AM) in relation to changes in soil chemistry and vegetation, and to variation in microclimate and soils operating at the landscape scale.

Assessing the abundance and activity of AM is difficult. Assessing AM abundance by counting spores or soil hyphae or determining the density of fungal structures in root fragments are all time- and effort-consuming, uncertain in precision, and, in the end, yield only indirect indices of AM fungal activity (Eom et al. 1999; Wright et al. 1996). In contrast, quantifying the AM fungus-specific glycoprotein glomalin shows promise as a direct measure of AM activity. Wright and Upadhyaya (1996) established that quantifiable amounts of glomalin are produced by AM fungi during active colonization of roots and during ramification of the mycelium in the soil. The deposition of glomalin as a result of AM fungal activity also contributes to the development of soil aggregates, which in turn leads to increases in soil aeration, drainage, root development, and microbial activity. Thus, production and deposition of glomalin represents a second, albeit indirect, mechanism by which AM fungi improve the performance of their plant hosts. In addition, quantifying glomalin content or production may afford ecologists what appears to be a robust method for assessing AM fungal activity in an ecological meaningful manner (Wright and Upadhyaya 1998, 1999).

Within this context, this study attempted to answer the following specific questions:

1. In the absence of fire, does the glomalin content of soils of oak-hickory forests remain relatively constant over 5- to10-year time periods?
2. In the absence of fire, does glomalin content vary among landscape positions, and is such variation most closely correlated with host plant density/diversity, with microclimate, or with soil chemical properties?
3. Does prescribed fire result in a change in glomalin content of soil directly through destruction or indirectly through postfire changes in nutrient availability and/or host plant density?
4. Can a predictive model for mycorrhizal activity (as measured by glomalin content) be constructed using soil chemical/physical properties and vegetation indices?

Materials and methods

Study site

The site chosen for this study was Arch Rock, located in Vinton County (latitude 39° 11'N, longitude 82° 22'W) on the Allegheny Plateau of southern Ohio. Arch Rock is a contiguous block of approximately 90 ha occupied by second-growth oak-hickory forests that developed following cutting for charcoal production in the 19th century (Sutherland and Hutchinson 2003). This site is one of four used for long-term prescribed fire and ecosystem restoration studies (Sutherland and Hutchinson 2003).

The tree stratum at this site is dominated by ectomycorrhizal species in the genera *Quercus* (oaks) and *Carya* (hickories) and AM species of *Acer* (maples) (Table 1). Shrubs are also abundant at this site and are dominated by AM species. The highly diverse herbaceous plant assemblage is also dominated by families that are typically AM (Table 1).

The soils of the study site are silt loam alfisols formed in colluvium and residuum from Pennsylvanian age sandstone and shale (Boerner and Sutherland 2003). These soils are relatively acidic and low in fertility: soil pH ranges from 3.7 to 4.7 and soil organic C content varies from 6 to 10%. Net N mineralization rate during spring ranges from 10–20 mgN/kg soil/day.

The climate of the study area is cool, temperate, continental, with mean annual precipitation and temperature of 1,024 mm and 11.3°C, respectively (Sutherland and Hutchinson 2003). Microclimatic gradients generated in the steep, dissected topography of the region produce within-watershed variation in conditions ranging from relatively xeric and infertile S-, SW- and W-facing upper slopes and ridgetops to relatively mesic and fertile N-, NE-, and E-facing lower slopes and valley bottoms (Wolfe et al. 1949).

Each of the three watersheds within Arch Rock was stratified using a GIS-based integrated moisture index (hereafter IMI) developed by Iverson et al. (1977) for this region. Areas occupied by three IMI classes (xeric, intermediate, mesic) were delimited within each watershed (Morris and Boerner 1998) and nine long-term sampling plots of 0.125 ha were established in a stratified random manner, with three of the plots in each of the three IMI classes.

To avoid concerns of pseudoreplication, intensive soil sampling was done during 1994 and 1995 to establish the pretreatment soil characteristics of each watershed and each IMI class within each watershed. There were no significant differences among the three watersheds or significant watershed-by-IMI class interactions in soil chemistry (e.g. pH, Ca^{2+}, Mg^{2+}, Al^{3+}, Ca:Al ratio, NH_4^+, NO_3^-, PO_4^{3-}), soil texture (e.g. particle size distribution, textural class), litter mass, soil organic C content, N mineralization rate, nitrification rate, or soil enzyme activities (Morris and Boerner 1998; Decker et al. 1999; Boerner and Sutherland 2003). Thus, we judged these three watersheds to be relatively uniform experimental material in which treatments could be assigned at random without pseudoreplication.

In April 1996, two of the three watersheds were chosen at random and burned. One of these watersheds was burned again in April of 1997 and 1998, and both burned watersheds were burned again in April 1999. Thus, we had one unburned control watershed, one which had been burned twice in 1996 and 1999 (hereafter 'periodically burned') and one which had been burned annually for 4 consecutive years (hereafter 'annually burned'). Analysis of fire behavior at these sites (Boerner et al. 2000; Hutchinson, unpublished data) demonstrated that these fires were patchy in intensity within a watershed, thus adding an additional aspect of independence to each of our sample plots.

Field methods

Soils for glomalin analysis were collected in October 1994 and May 2000 from random points near the opposite corners of each 0.125 ha sampling plot. The soils were air-dried to constant mass, then stored in sealed plastic bags in the dark at room temperature

pending analysis. Thus, the 1994 samples were stored for approximately 7 years prior to analysis, while those from 2000 were stored for approximately 1 year. A total of 108 samples (2 sample years × 3 treatment units × 9 sampling plots/treatment unit × 2 samples/sampling plot) were analyzed as part of this study. Subsamples were also used for analysis of inorganic soil chemical parameters (Boerner 2000) and N mineralization/nitrification (Boerner et al. 2000).

Laboratory methods

Easily extractable glomalin (EEG) and total glomalin (TG) were extracted from 1-g subsamples with citrate buffers using the methods of Wright and Uphadyaya (1996, 1998). The EEG and TG fractions were then tested for immunoreactivity with an ELISA using the monoclonal antibody MAb32B11. The antibody was raised against crushed spores of the fungus *Glomus intraradices* and reacts with extracts of a range of AM fungi (Wright and Uphadyaya 1996). The immunoreactive fractions of EEG and TG are termed IREEG and IRTG.

Data analysis

All glomalin concentration data were tested for normality and homogeneity of variances but none required transformation to meet the assumptions of the analysis of variance. We used statistical tests specifically designed to test each of the three specific questions posed earlier rather than relying on a global, four-way analysis of variance.

To determine whether glomalin content was stable over time in the absence of fire, we considered only the data from the sampling plots in the unburned controls, and used a one-way analysis of variance with sample year as the main effect. To determine how glomalin content varied with landscape-scale variation in microclimate, we considered only the data from the 1994 sampling and used a one-way analysis of variance with IMI class as the main effect. Although we could have used a two-way anova with IMI class, treatment unit, and their interaction as effects, the extensive analysis our group has done on other soil chemical and biological parameters on this site has demonstrated a lack of significant differences among watersheds within study sites (Decker et al. 1999; Boerner et al. 2000; Boerner and Sutherland 2003), thus obviating the need to consider among watersheds in this test. To determine whether fire affected glomalin content significantly, we focused on the data from the sampling year 2000, and used a one-way analysis of covariance with fire treatment as the main effect and pre-treatment (1994) glomalin content as a covariate. Thus, we focused on variation in glomalin content after fire in relation to prefire glomalin content of those same sampling points, thus eliminating pseudoreplication concerns. To determine whether there were interactions between fire and landscape position, we repeated the ancova with the addition of a second main effect (landscape position = IMI class) and the interaction of fire and landscape position. We also performed Pearson Product-Moment correlation analyses utilizing the glomalin contents from 1994 and 2000, soil chemical data from those same samples (pH, NH_4^+, NO_3^-, PO_4^{3-}; data from Boerner 2000; Boerner and Sutherland 2003) and vegetation data from the permanent sampling plots adjacent to the soil sampling points (herbaceous species richness, density of AM host woody plant species, percent of AM hosts among the woody species present; data from Hutchinson et al. 1999, Yaussy, unpublished data). In an attempt to produce a predictive model for soil glomalin content, we also used forward selection stepwise regression using glomalin content as the independent variable and the same suite of dependent variables.

The SAS system (SAS 1995) was used for all statistical analyses. All differences indicated as significant were at $P<0.05$, except where noted otherwise. The Ryan-Einot-Gabriel-Welsch Modified F-test (SAS 1995) was used to separate means where significant differences were indicated by anova or ancova. This post-test was chosen because it minimizes Bayes risk and the probability of type I errors.

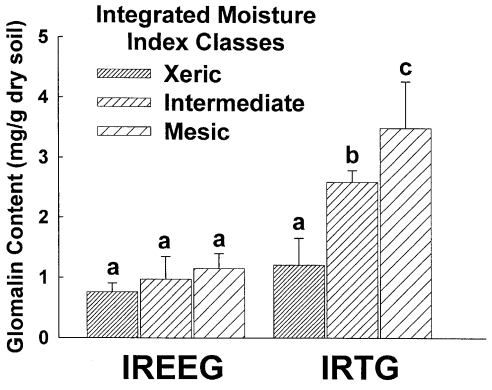

Fig. 1 Concentrations of immunoreactive, easily-extractable (*IREEG*) and total (*IRTG*) glomalin in forest soils in relation to long-term soil moisture potential (integrated moisture index classes). For each histogram bar $n=18$; standard errors of the means are indicated. Histogram bars labeled with the same lower case letter are not significantly different at $P<0.05$

Results

There were no significant differences in glomalin content of soils between 1994 and 2000 in the unburned controls. IREEG and IRTG content of the soils from the controls averaged 0.67 (± standard error 1.01) and 1.28 (±1.48) mg/g soil, respectively in 1994, and 0.81 (±1.08) and 1.28 (±1.54) mg/g soil, respectively in 2000. Thus, in the absence of fire or disturbance, glomalin content of the soils of these aggrading, second-growth forests did not appear to change over 6 years.

There were no significant differences in IREEG content among IMI classes ($P>0.504$; Fig. 1). In contrast, there were significant differences in IRTG content among IMI classes ($P<0.048$), with IRTG content increasing from xeric to mesic (Fig. 1). We found neither an effect of fire nor an interaction of fire with landscape position for either IREEG or IRTG.

Over both sampling years, IREEG was significantly and positively correlated with soil N availability (NO_3^-: $r=0.42$, $P<0.01$; NH_4^+: $r=0.36$, $P<0.01$), but not soil pH, soil P availability, or any of the characteristics of the plant assemblage we tested. In contrast, IRTG was significantly and positively correlated with soil N plot (NO_3^-: $r=0.60$, $P<0.01$, NH_4^+: $r=0.62$, $P<0.01$) and also with soil pH ($r=0.34$, $P<0.02$), the density of AM host plants ($r=0.34$, $P<0.04$) and the diversity of herbaceous plant species in the sample plot ($r=0.36$, $P<0.01$). The correlations of IRTG with soil N concentrations were approximately twice as strong as the correlations with host plant attributes. Although IREEG was not correlated with available P either in the pooled data set or in either of the individual year data sets, IRTG content was positively correlated with soil P in 1994 ($r=0.56$, $P<0.01$) but

Table 1 Vegetation of southern Ohio research sites, stratified by integrated moisture index (*IMI*) class. All data are from 0.125-ha permanent sampling plots (n=10 for xeric, n=6 for intermediate, and n=11 for mesic). Data from Hutchinson et al. (1999) and Hutchinson, unpublished data

IMI class	Tree diversity (no. of species per plot)	Most abundant tree species	Most abundant shrub/vine species	Herbaceous diversity (no. of species per plot)	Most abundant herbaceous families
Xeric	7.2	*Quercus alba*[b]	*Smilax rotundifolia*[a]	30.8	Fabaceae[a]
		Quercus prinus[b]	*Vaccinium pallidum*[c]		Poaceae[a]
		Quercus velutina[b]	*Smilax glauca*[a]		Asteraceae[a]
		Acer rubrum[a]	*Rubus* spp.[a]		Cyperaceae[c]
		Carya spp.[b]	*Rosa carolina*[a]		
Intermediate	8.5	*Quercus alba*[b]	*Parenthocissus quinquefoilius*[a]	39.4	Poaceae[a]
		Acer rubrum[a]	*Viburnum acerifolium*[a]		Fabaceae[a]
		Carya spp.[b]	*Rubus* spp.[a]		Asteraceae[a]
		Quercus prinus[b]	*Smilax rotundifolia*[a]		Lamiaceae[a]
		Nyssa sylvatica[a]	*Lindera benzoin*[a]		
Mesic	9.6	*Quercus alba*[b]	*Parenthocissus quinquefoilius*[a]	45.5	Lamiaceae[a]
		Acer rubrum[a]	*Virburnum acerifolium*[a]		Asteraceae[a]
		Carya spp.[b]	*Rubus* spp.[a]		Liliaceae[a]
		Nyssa sylvatica[a]	*Smilax rotundifolia*[a]		Fabaceae[a]
		Fagus grandifolia[b]	*Toxicodendron radicans*[a]		

[a] Arbuscular mycorrhizal
[b] Ectomycorrhizal
[c] Other mycorrhizal relationships

negatively correlated with soil P in 2000 (r=-0.66, P<0.01).

Stepwise regression resulted in multiple regression models for glomalin content that were statistically significant, but poor in predictive strength. The best-fit model for IREEG was based on IMI, herbaceous plant diversity and the proportion of AM hosts among the woody plants present (Table 2). However, this model could explain only 11% of the variation in IREEG among samples. The best-fit model for IRTG was somewhat stronger (r^2=0.24), and was based on IMI, herbaceous plant diversity and soil NO_3^- (Table 2).

Discussion

Our overall objective was to determine whether low-intensity, dormant season fire has an effect on the activity of AM in the deciduous forest ecosystems of eastern North America. We also hoped to determine whether such fire effects vary across the landscape, and to develop a predictive model for mycorrhizal activity based on easily quantifiable soil and vegetation attributes.

We found no significant differences in the content of either easily extractable IREEG or IRTG between samples taken from control sites in 1994 and 2000. This suggests that the rates of glomalin production and degradation were approximately equal over that time period, though we have no way to calculate the absolute rates of either production or degradation from our experimental data.

Of more interest may be the rate at which the relatively labile IREEG is degraded versus incorporated into more recalcitrant physical or chemical forms such as IRTG. In our soils, the IREEG fraction was 52–63% of the IRTG fraction. If the turnover rate for IRTG is similar to the turnover rate of 6–42 years estimated by Rillig et al. (2001a) for Hawaiian forest soils (and this may well not be the case), IREEG degradation by microbes at our sites must be rapid for the IREEG:IRTG ratio to be so high at any one point in time. That, in turn, suggests high activity of AM fungi in these soils. This is consistent with the high intensity of AM infection of herbaceous plants (e.g. Boerner 1986; DeMars and Boerner 1995), high total fungal activity (Morris and Boerner 1998; Morris 1999), and rapid turnover rate of fungal tissues (Friese and Allen 1991) at these and other sites. In turn, as glomalin production is strongly tied to the development of water-stable soil aggregates (Rillig et al. 2001b, 2002), these forest soils should be strongly aggregated; we are currently analyzing fresh soil samples to test this. Although we postulate on these bases that AM fungal activity is relatively high in these forested sites, robust estimates of the rates of IREEG production, IREEG degradation, and the conversion of IREEG to IRTG require experimental manipulations beyond the scope of this initial study.

We found a significant relationship of IRTG content with landscape position (as measured by the IMI index of

Table 2 Forward selection stepwise regression of the content of two fractions of glomalin (immunoreactive, easily-extractable glomalin (*IREEG*), immunoreactive total glomalin (*IRTG*) on environmental site variables. Independent variables tested included IMI, soil organic C, NO_3^-, NH_4^+, total inorganic N, PO_4^-, Ca^{2+}, Al^{3+}, sand fraction, clay fraction, diversity of herbaceous plants, density of AM-host woody plants, and the proportion of all woody plants that were AM fungal hosts. Only variables that entered the model at $P<0.05$ are included, and all listed entered as positive relationships. The probability level (P) and coefficient of determination (r^2) are given for each variable and for the overall model (n=54)

Variance component	IREEG	IRTG
IMI	Partial r^2=0.05 P<0.01	Partial r^2=0.02 P<0.01
Herbaceous plant diversity	Partial r^2=0.02 P<0.0’	Partial r^2=0.08 P<0.01
Proportion of AM hosts among woody plants present	Partial r^2=0.03 P<0.01	Not significant –
Soil NO_3^-	Not significant –	Partial r^2=0.14 P<0.01
Full model	r^2=0.11 P<0.01	r^2=0.24 P<0.01

Iverson et al. 1997). The soils of mesic, lower-slope sampling plots had the highest IRTG content. Intermediate IMI class soils averaged 15% less and upper-slope/ridgetop soils 34% less IRTG than mesic soils. This pattern of variation correlates well with that of host plant distribution. In this region, the density and diversity of herbaceous plants, most of which are AM dependent, increase downslope (Hutchinson et al. 1999; Hutchinson, personal communication), as does the proportion of tree species that depend on AM fungi as opposed to ectomycorrhizal (ECM) fungi (Hutchinson et al. 1999). In addition, N availability is greatest in mesic IMI class soils (Boerner et al. 2000; Boerner and Sutherland 2003). DeMars and Boerner (1995) reported highest mycorrhizal fungal infection in forest plants in positions along topographic gradients where N availability was highest, and also found no relationship between mycorrhizal infection and P availability. We believe our results and those of DeMars and Boerner (1995) emphasize the need to consider AM fungal activity not solely in terms of P availability, but rather in terms of the relative availability of N and P. To maintain cytoplasmic N:P ratios, plants and microbes growing in high N soils will need to exert a strong demand for P in order to take advantage of the available N. For plants, this typically means maximizing carbon allocations for AM activity. The fact that the only significant, positive correlations we found between glomalin content and site factors were with soil N and host plant density/diversity supports this view.

It is interesting to note that neither fraction of glomalin reached a maximum in the ridgetop, xeric IMI class soils, which are the lowest in available P in our study sites. This may be because of a higher proportion of woody plants present on ridgetops being dependent on ECM fungi, or because of lower total plant density in the dry infertile ridgetop soils, or both.

We found no direct evidence for an effect of low-intensity, dormant season fire on glomalin content after 2–4 fires. This was surprising to us, as previous studies have demonstrated significant increases in soil pH (Boerner 2000) and N mineralization (Boerner et al. 2000) in burned plots, as well as significant reductions in spring root production (Dress and Boerner 2001). Boerner et al. 2003 also reported increased activity of chitinase in soils of burned plots, although it has not been determined whether this is a response by chitinolytic bacteria to increased production of fungal tissue, the death of large numbers of microarthropods in the annually burned plots (Dress and Boerner 2002), or to changes in the quality of soil organic C.

Despite these ecologically significant changes in the chemistry and biochemistry of the soils of these forested sites, there have been only modest changes in the vegetation, and little change in the herbaceous, ground-layer vegetation that dominates plant numbers. The lack of any significant change in glomalin fractions may be simply a reflection of the strong resistance that the flora exhibits in the face of low-intensity, dormant season fire. Alternatively, as glomalin is extremely heat stable, it may not be directly affected by low-intensity fires, during which temperatures in the top 10 cm of mineral soil increase only transiently if at all, and even then by no more than 5–10°C (Boerner 2000). Such transient heating events are not even sufficient to kill active fungal hyphae. Thus, effects of fires on AM hyphae in soil and on glomalin already present are not likely to be detectable against the background glomalin concentrations in soil (i.e. small flux, large pool problem). However, as we measured only static content, we cannot rule out the possibility that both the glomalin production and degradation rates were increased or decreased significantly by fire, which had no effect on the static pool size.

Although we were able to construct statistically significant regression models for predicting IREEG and IRTG content based on soil chemical parameters and characteristics of the vegetation, the models are quite weak in predictive strength. Only 11–24% of the variation in glomalin fractions could be predicted with these models. One might interpret this as a failure of our design to include measurement of key variables driving

glomalin production and accumulation. Instead, we suggest that the weakness of these models is the result of a combination of high variability in glomalin content among samples and the relatively narrow range over which most of our soil chemical parameters and vegetation characteristics varied. Rillig et al. (2001a) were able to produce much stronger relationships, and did so in an environmental context where the soil variables they measured varied considerably more than they did in our study. Large variation in a dependent variable coupled with low levels of variation in putatively causal independent variables is a classic recipe for a weak regression model.

This study has succeeded in establishing baseline content for the immunoreactive EEG and TG fractions in oak-hickory forests in relation both to strong gradients of microclimate and to relatively low-intensity disturbance. However, how the subtle changes in the below-ground parts and processes of these ecosystems influence both plants and their fungal symbionts over the longer periods of treatment necessary for ecosystem restoration remains to be determined.

Acknowledgements This study was funded by a grant from the USDA Forest Service Ecosystem Management Program. We thank Elaine Kennedy Sutherland for project leadership and permission to use the field site, Sherri Jeakins Morris, Kelly Decker, William Dress, Jennifer Brinkman, and Rachel Thiet for field assistance, Emily Lutgen and Peter Steinberg for laboratory assistance, and Serita Frey and Landon Rhodes for comments on earlier versions of this manuscript.

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