Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management xxx (2007) xxx–xxx
Forest Ecology and Management
www.elsevier.com/locate/foreco

Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico

Helen A. Violi [a,f,*], Alejandro F. Barrientos-Priego [b], Sara F. Wright [c], Esteban Escamilla-Prado [d], Joseph B. Morton [e], John A. Menge [f], Carol J. Lovatt [a]

[a] *Department of Botany and Plant Sciences, University of California, Riverside, CA 92521, USA*
[b] *Departamento de Fitotecnia, Universidad Autónoma Chapingo, Chapingo, Mexico*
[c] *U.S. Department of Agriculture, ARS-Soil Microbial Systems Lab, Beltsville, MD 20705, USA*
[d] *Universidad Autónoma Chapingo, CRUO (Centro Regional Universitario Oriente) Huatusco, Veracruz, Mexico*
[e] *West Virginia University, Division of Plant & Soil Science, Morgantown, WV 26506, USA*
[f] *Department of Plant Pathology, University of California, Riverside, CA 92521, USA*

Received 22 May 2007; received in revised form 8 August 2007; accepted 11 August 2007

Abstract

Mexican montane rainforests and adjacent disturbed areas were studied for disturbance-related spatio-temporal changes to the arbuscular mycorrhizal fungal (AMF) community and soil glomalin concentration. The AMF community functions to both improve plant growth and soil conditions and is thus an important component to the restoration of this forest type to disturbed areas. The study areas included mature rainforests that were converted to pine forests, milpas, pastures and shrub/herbaceous plant communities via burning and logging. Seasonal patterns in AMF spore species richness and sporulation significantly differed across disturbance types at two of the three sites surveyed. Contrasting patterns of sporulation among AMF families across different disturbance types helped to explain how species richness and composition were maintained despite dramatic changes to the host plant community. Meaning, in most cases, disturbance induced changes in when different AMF taxa sporulated but not what taxa sporulated. Only conversion from mature pine–oak–*Liquidambar–Persea* forests to pine-dominated stands severely reduced AMF spore richness and total sporulation. Surprisingly, in pine-dominant stands no concomitant negative impacts on soil glomalin (MAb32B11 immunoreactive soil protein) concentrations were detected. However, soils of mature forests containing no pines had the highest concentration of glomalin. Conversion to pasture and milpa (diverse cornfield) had a strong negative impact on the concentration of soil glomalin concentrations. In sharp contrast, the same disturbance types improved AMF sporulation and AMF spore richness. It appears that disturbance type, and not AMF community measures used herein, best predicts changes in soil glomalin concentration.

Keywords: Glomalin; MAb32B11 immunoreactive soil protein; Mycorrhizal fungi; Mexico; Montane rainforest; Sporulation; Phenology; Disturbance

1. Introduction

Arbuscular mycorrhizal fungi (AMF) belong to a unique lineage (phylum Glomeromycota) that is hypothesized to be among the oldest terrestrial organisms (Pawlowska, 2005). The mycorrhizal association, although obligate for the fungal symbiont, is widespread because host range encompasses at least 80% of all land plants (Trappe, 1987). Ordovician fossils of morphologically equivalent fungi in non-vascular plant tissue and phylogenetic relationships among AMF lineages provide some evidence that these obligate symbionts have changed little in relation to the radiation of their plant hosts (Morton, 1990; Redecker et al., 2000). The number of known species based on morphological traits is less than 200, which likely is due more to constraints on available morphospace diversity (Morton et al., 1995) than ecological constraints (Law,

* Corresponding author. Present address: USDA ARS SHRS, 13601 Old Cutler Road, Miami, FL 33158, USA. Tel.: +1 786 554 2682; fax: +1 305 969 6410.
E-mail address: hvioli@ufl.edu (H.A. Violi).

0378-1127/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2007.08.016

1985). It would appear that the long-term evolutionary stability of the AM symbiosis can be attributed to remarkable resilience by AMF populations and possibly even species, a wide host range, and the ability to grow under a broad set of environmental conditions.

To support the symbiosis, plants are estimated to allocate 4–20% fixed carbon to AMF (Graham, 2000), which can comprise as much as 50% of the soil microbial biomass (Olsson et al., 1999). Arbuscular mycorrhizal fungal biomass is in part glomalin, a soil protein that is contained in AM hyphal walls and hypothesized to turnover slowly in natural systems (Steinberg and Rillig, 2003). Glomalin is operationally defined and largely separated from humic substances when measured using the monoclonal antibody MAb32B11 in an enzyme-linked immunosorbent assay (ELISA) (Nichols and Wright, 2006; Rosier et al., 2006). It is estimated that between 355 and 45% of glomalin is carbon (Lovelock et al., 2004; Nichols and Wright, 2006; IHSS, 2006) and that soils in temperate forest systems contain between ~2 and 15 mg g^{-1} soil glomalin (Rillig, 2001), implying that a significant amount of fixed carbon may be allocated by AMF to glomalin production. Thus, enhanced nutrient uptake is not the only function of the AMF symbiosis. AMF-derived glomalin can accumulate in soil and improve soil structure to the benefit of plants (Franzluebbers et al., 2000; Rillig et al., 2002; Rillig and Steinberg, 2002; Rillig and Mummey, 2006). Common disturbances, such as deforestation, can alter AMF communities (Stahl et al., 1988; Jasper et al., 1991), but the impact of these changes on the soil environment and, hence, on forest succession are poorly understood (Hart et al., 2001; Rillig, 2004; Urcelay and Díaz, 2003).

In montane forests common disturbances (such as burning, logging, conversion to pasture, or agricultural field) can significantly alter the proportion of mycotrophic versus nonmycotrophic plant species in a community (Ochoa-Gaona and González-Espinosa, 2000). These changes, in turn, can affect dynamics of the AMF community and its sporulation patterns. For instance, in montane oak–pine forests of Mexico, broad-leaved tree species often are removed in favor of pines or forests are converted to pasture or milpa (diverse cornfield) (Ochoa-Gaona and González-Espinosa, 2000; Ramirez-Marcial et al., 2001). The latter disturbance types do not necessarily reduce the diversity of AM plant species but often create long fallow periods (Tacher et al., 2002; Brush et al., 2003; Muniz-Castro et al., 2006). High-till agricultural practices combined with long fallow periods often negatively impact abundance and diversity of AMF sporulation in field soils (Jansa et al., 2002; Azcón-Aguilar et al., 2003). Alternatively, some severe disturbances leading to the establishment of pastures and milpas may positively impact AMF community diversity (Johnson and Wedin, 1997; Picone, 2000). Regardless, such changes may have strong effects on spatio-temporal patterns in AMF sporulation (Azcón-Aguilar et al., 2003) and consequently AMF function. Disturbance can negatively impact soil structure through physical disruption and by altering the plant and AMF community. The consequences of soil disruption are particularly severe on the steep slopes of montane forests.

For trees belonging to some of the dominant families in Mexican montane forests (Fagaceae, Pinaceae and Betulaceae), ectomycorrhizal fungi form the dominant mycorrhizal associations (Smith and Read, 1997). Specifically, pines are solely ectomycorrhizal, *Quercus* species can form both ectomycorrhizal and AM associations, but *Liquidambar* and tree species in Lauraceae form only AM associations (Alexopoulos et al., 1996). Selective logging activities and burning typically favor early colonizing ectomycorrhizal trees within many Mexican montane forests (Ochoa-Gaona and González-Espinosa, 2000; Ramirez-Marcial et al., 2001), suggesting that AM associations would be less prevalent.

Glomalin as well as AMF hyphae contribute to improved soil quality by promoting soil aggregation (Rillig et al., 2003). Glomalin concentrations correlate highly with soil aggregate stability in many soil types (Wright and Upadhyaya, 1998; Wright and Anderson, 2000). Evidence suggests that the capacity to synthesize glomalin varies among AMF species (Wright and Upadhyaya, 1999). Severe disturbance and/or disturbance-related shifts in the proportion of ectomycorrhizal to AM plant species may impact soil glomalin concentration, which in turn may be regulated somewhat by AMF species composition and abundance. Disturbance can also reduce glomalin accumulation and hence the stability and degree of soil aggregation (Wright et al., 1999). Limited evidence suggests that some types of disturbance, such as fire, do not negatively impact soil glomalin concentrations (Knorr et al., 2003). Examining disturbance-related changes in AMF species richness, community composition, abundance of sporulation and soil glomalin concentration may improve our understanding of AMF community dynamics following disturbance. A better understanding of AMF community dynamics will enhance our ability to manage AMF to improve soil structure and prescribe where and when soil for AMF inoculum production should be collected for reforestation efforts in this region.

Therefore, the main objective of this paper was to examine community-level spatio-temporal patterns of AMF sporulation and soil glomalin concentrations to answer the following questions: (i) are there spatio-temporal differences in AMF spore richness, composition and abundance among mature forests and adjacent disturbed areas? and (ii) are soil glomalin concentrations affected by disturbance?

2. Materials and methods

2.1. Site descriptions

Study questions were answered separately for four locations, each including a mature forest with adjacent disturbed areas (Table 1). We selected mature montane forests that were floristically similar and each forest was juxtaposed to areas that had been disturbed a minimum of 5 years and a maximum of 10 years prior to the study. Forests can be referred to as montane rainforests, tropical montane cloud forest or bosque mesófilo de montaña (Rzedowski, 1978). Disturbance types chosen are the most common to the region and are burned areas, forests

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

Table 1
Site characteristics for study areas in Chiapas and Veracruz, Mexico

Site name	Bazom	Tzontehuitz	Centro Regional Universitario Oriente (CRUO)	La Cascada
Mexican city state	Chiapas	Chiapas	Veracruz	Chiapas
Disturbance types adjacent to mature forests included in the study	Milpa, pine forest	Pine forest, burned areas, semi-logged areas	Pastures	Burned areas
Elevation (m a.s.l.)	2300–2448	2750	1200–1344	2796
Seasons in which soil was sampled	Winter (early March), summer (August) and fall (early November)	Winter (December), summer (August) and fall (October)	Rainy (September), dry season (February) and summer (early July)	Winter (December)
Wettest months	June and September	Varies, May through October	September	Data not available
Dominant mature forest tree genera	Persea-Quercus-Pinus	Persea-Quercus-Liquidamber	Several lauraceous genera-Quercus-Liquidamber	Persea-Phoebe-Ocoteo
Average annual precipitation (mm)	1100–1600	2000	1700	2500–4500
Climate	Subhumid temperate (occasional winter frosts)	Subhumid temperate (occasional winter frosts)	Semitropical (no winter frosts)	Subhumid temperate (occasional winter frosts)
Average annual temperature (°C)	Ranges between 13 and 17	14.7	17.7	Ranges between 14 and 18

converted to pine-dominant stands, milpas, non-selectively logged forests and/or pastures (Cayuela et al., 2006). Study sites were at three different locations in the highlands of Chiapas and one in Huatusco, Veracruz (Fig. 1). For data on the AMF spore community, all statistical analyses were performed among mature forests and adjacent disturbed areas and no statistical comparisons were made between disturbed areas at different geographic locations.

In Chiapas, three locations were selected for study: La Cascada (or Siltepec) near Motozintla, the ejidos Rancho Merced Bazom and Tzontehuitz, both near San Cristóbal de las Casas. The site has very steep slopes and forests dominated by lauraceous trees in the genera *Persea*, *Phoebe* and *Ocoteo*. Adjacent burned areas were primarily dominated by grasses and herbaceous species in the families Asteraceae and Laminaceae.

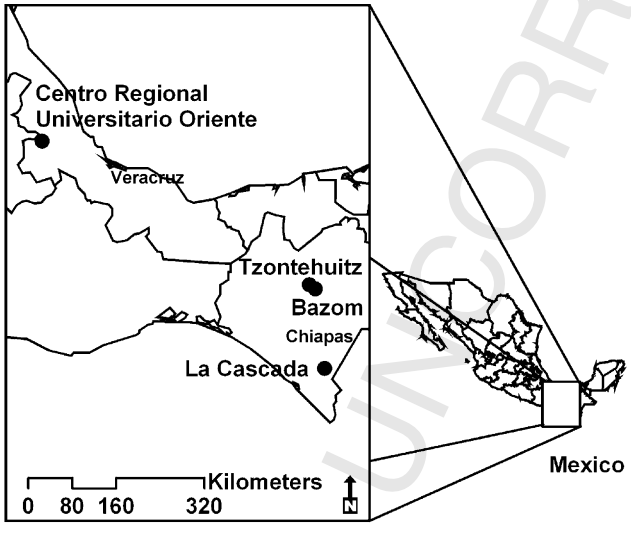

Fig. 1. Locations of study sites in Chiapas and Veracruz, Mexico. Each mature forest chosen for the study was juxtaposed to disturbed areas that represented common disturbance types for the region. Mature forests (each with adjacent disturbed areas) were located in the ejido Bazom (16°44′N and 92°29′W), the ejido Tzontehuitz (16°48′N and 92°35′W), La Cascada (or Siltepec) (15°26′ and 92°20′W) and at the Centro Regional Universitario Oriente (CRUO) near Huatusco, Veracruz (19°9′N and 96°57′W).

The disturbance types at the Bazom ejido included milpas, pine forests and burned areas. Milpas are dominated by *Zea mays*, *Phaseolus vulgaris* and a wide diversity of herbs and composites for 5–8 months of the year. During the remainder of the year the fields are in fallow. All forests within this ejido and surrounding forests included pine as an important upper canopy tree species. The forests here included Pinus-Quercus-Persea mature forests (ba-mf), Pinus-Quercus-Liquidamber (site named c-pf) and pine mono-dominant stands (sites named sjf-pf and oc/mi-pf). The c-pf site was used to collect glomalin data but not AMF spore data.

The site located in Tzontehuitz is dominated by *Liquidamber styraciflua*, *Persea americana* var. *steyermarkii* and *Quercus* spp. Burned areas were dominated by a large diversity of ferns and shrubs. Logged forests were also high in fern diversity, resprouting *Quercus* and a shrub species composition similar to that of other burned areas. Shrubs included species within the families Caprifoliaceae, Rosaceae, Asteraceae and Zygophyllaceae. Soils are shallow (<50 cm) and of complex of sedimentary and volcanic origin including lythosols and rendzines (Mera-Ovando, 1989). Mean annual precipitation is 2000 mm (Ramirez-Marcial, 2003). Most areas are inundated with fog 4–8 h daily (Zuill and Lathrop, 1975).

In Huatusco, Veracruz, the study was located within the Centro Regional Universitario Oriente (CRUO) station and included a mature forest area and two pastures with slopes ranging from 20 to 60% (Montiel and Robledo, 1998). The mature forest is semitropical (bosque mesófilo de montaña) and dominated by *Quercus* spp., *Eugenia xalapensis*, *L. styraciflua*, *Phoebe* spp. and *Turpinia insignis*. Pasture areas were dominated by grasses, sedges and herbaceous plants including *Paspalum* spp., *Setaria* spp., *Cynodon dactylon*, *Plantago major*, *Eragrostis* spp. and *Cyperus* spp. The majority of rainfall occurs between June and October, September being the wettest with an average of 393.7 mm (Montiel and Robledo, 1998). A dry season typically occurs between February and

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

June. March is usually the driest month within the dry season with an average of 30.9 mm of rain (Montiel and Robledo, 1998). Between October and February, periods of below average annual temperatures and high winds, referred to as the ''nortes'', commonly occur. AMF sampling was performed once during the dry season (February), the rainy season (September, also known as the ''nortes'') and in the summer (July). Soils are classified as andosoles with a mollic horizon in mature forests. These soils are derived from igneous intrusive rock and include thick deposits of volcanic ash (Montiel and Robledo, 1998).

2.2. Soil sampling

All sites were divided into three blocks based on slope, aspect and/or plant species composition. Soil samples from each block were collected at random locations along two 10 m transects. All soil samples were collected from the upper 10 cm of soil and eight samples per transect were collected to estimate glomalin concentrations in the soil. These samples, ca. 100 ml each, were collected in groups of four samples from the four corners of a 4 m^2 area. The location of each 4 m^2 area was determined by randomly selecting a point on either side of the transect. Sixteen samples (25 ml) per block (48 samples per site) were used for glomalin analysis. For trap cultures (see definition in Section 2.3) and for extracting AMF spores, composite samples were created. Composite samples were created by combining and then homogenizing groups of four samples with the remaining soil (50 cm^3 of soil from each 4 m^2 area) for two composite samples per transect. A total of six composite samples were analyzed per site per sampling period to detect seasonal changes to AMF spore number, richness and composition. Thus, 24 samples were combined into six per sampling period per site. An additional five composite samples were collected for producing trap cultures. One exception was La Cascada, where only one collection period was possible in December due to cutting and burning.

2.3. AMF community measurements

Spores were extracted from indigenous soil using a wet sieving (nested sieves of 40–500 μm pore size) technique followed by sucrose extraction (Dalpe, 1989). To better characterize total AMF richness, trap cultures were used and species detected in trap cultures but not in the field were added to the total AMF richness estimates per site. Trap cultures are used both to induce sporulation of species not detected in field samples and to acquire healthy spores for identification purposes. Traps were sown with alfalfa (*Medicago sativa*) in 0.2 l samples of indigenous soil from each site mixed with 0.8 l of sterilized sand (autoclaved for two 1 h periods over 24 h). At 6 months, watering was discontinued and the alfalfa was allowed to senesce for 1 week. AMF spores were then extracted from 0.1 l of soil using the same methods described for indigenous soil. Spores were then isolated on grid-lined cellulose membranes (MF-Millipore, Millipore Corporation, Bedford, MA, 47 mm diameter, 0.45 μm pore size), categorized based on size and color, and counted under a dissecting microscope.

For identification, spores were placed on microscopic slides, stained with Melzer's reagent and/or mounted in polyvinyl-lacto-glycerol (PVLG) according to category and observed under a compound microscope. These methods were modified after those described in Schenck and Perez (1990). AMF spore identity was determined using descriptions published in Schenck and Perez (1990) and other descriptions published after 1990. For AMF spores that were detected in field samples and in trap cultures that could not be adequately described by existing references, written descriptions are included herein. Where multiple conflicting descriptions existed, the most conservative approach was employed (i.e., lumped rather than split species as not to inflate estimates of species richness or diversity based on minor differences in spore morphology). In the several cases, too few spores from field samples and or multispore trap cultures existed to properly identify AMF to species; a ''morphospecies'' label was used.

2.4. Quantification of soil glomalin and soil analysis

Glomalin was extracted from soil samples by autoclaving in 8 ml of 50 mM sodium citrate buffer (pH 8.0) for 60 min. The cooled extract was centrifuged at 6000 rpm for 15 min (Wright et al., 1996). The precipitate was extracted two additional times. The supernatants from each extraction were pooled. First, total protein (excluding heat labile proteins that do not survive the extraction process) was determined using the Bradford assay (Bio-Rad Laboratories, Richmond, CA). The concentration of total protein extracted from each sample was determined by comparison with bovine serum albumin (BSA) as the standard. The Bradford assay was not used to directly estimate glomalin concentrations, but total protein estimates were used to dilute samples into a range in which in glomalin concentration (mg g^{-1} fresh wt soil) could be more accurately estimated using the monoclonal antibody MAb32B11 in an enzyme-linked immunosorbent assay (ELISA) (for further details on methods see Wright and Upadhyaya, 1996). In this paper we refer to the MAb32B11 immunoreactive fraction as simply ''glomalin''. Another recently proposed term for this fraction is ''immunoreactive (MAb32B11) soil protein'' (Rillig, 2004).

For soil analyses, six composite samples per disturbance type (composite samples were created as described in Section 2.2) were pulverized to pass through a 2 mm sieve. Samples were analyzed for organic carbon, organic matter, and Bray-P using DTPA extraction (diethylenetriaminepentaacetic acid). The soil parameters were measured by the University of California Agricultural and Natural Resource Analytical Laboratory (University of California, Davis, CA) according to standard methods (Table 2).

2.5. Statistical analysis

All analyses were performed in JMP 5.1.1 (JMP, Version 5.1.1, SAS Institute Inc., Cary, NC, 1989–2002). All statistical analyses for AMF spore community data were performed

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

Table 2
Means for total organic C, P and % organic matter (OM)

Disturbance type	Total C (%)	Bray-P (ppm)	OM (%)
ba-mature forest	14.90 (0.68)	42.18 (8.17)	38.54 (4.87)
ba-milpa	4.98 (0.26)	9.83 (3.25)	7.60 (0.11)
ba-milpa2	5.16 (0.13)	3.85 (0.24)	6.68 (0.52)
c-pine forest	21.45 (1.89)	23.25 (4.96)	43.68 (7.82)
lc-burn	11.28 (1.23)	80.23 (26.91)	18.52 (4.29)
lc-mature forest	19.51 (4.05)	83.77 (31.88)	45.70 (7.27)
oc/mi-pine forest	13.77 (1.54)	11.93 (3.35)	40.60 (8.73)
sjf-pine forest	7.02 (0.56)	8.57 (2.57)	18.77 (3.36)
tz-burn	13.51 (1.85)	5.53 (2.40)	32.92 (3.40)
tz-log	19.75 (3.73)	88.08 (51.44)	52.12 (7.98)
tz-mature forest	20.92 (4.65)	139.33 (45.99)	47.50 (5.98)
v-mature forest	25.23 (2.25)	4.15 (2.10)	52.60 (2.93)
v-pasture agri	5.84 (0.30)	6.02 (1.28)	10.04(0.61)
v-pasture cafe	6.39 (0.37)	1.16 (0.34)	8.60 (0.23)

Standard errors of the means are given in parentheses. Sites (tz = Tzontehuits, lc = La Cascada, v = Centro Regional Universitario Oriente in Veracruz, oc/mi, c, sjf and ba are all sites in or near the Bazom ejido) and disturbance types [mature forest, burned area (burn), non-selectively logged area (log), pine forests (which were selectively logged), pasture and milpa] were based on site history (last 10 years) and plant composition ($n = 6$).

among mature forests and adjacent disturbed areas. No significant differences in means for any of the AMF spore variables examined between the two milpas, the pine forests or the two pastures were detected within the Bazom or Veracruz sites. Thus, these data were pooled by disturbance type within each site for further analysis. To determine if seasonal patterns in spore number (a measure of infectivity) and AMF species richness contrasted across disturbance types, a univariate standard least squares model was used. To determine if there were seasonal differences in the AMF community composition among mature forests and adjacent disturbed areas, a multivariate regression was performed and an identity matrix was chosen. In this analysis, seasonal sporulation by AMF family was examined across disturbance types and seasons for each site.

One-way univariate standard least squares analysis was performed to test for differences in the glomalin concentration between disturbance types. Significant differences in glomalin concentrations were detected between the different milpas, pine forests and pastures sampled. Thus, for glomalin, each milpa, pine forest and pasture was treated separately.

Pairwise comparisons among disturbance types within sites were performed using Tukey–Kramer HSD (JMP, Version 5.1.1, SAS Institute Inc., Cary, NC, 1989–2002). *t*-Tests were used where only two disturbance types were compared (La Cascada). Samples collected from individual transects were treated as ''blocks'' (see Section 2.2 for a description of the blocks) and tested for significant differences within each site by including ''block'' as a term in the ANOVA.

3. Results

3.1. AMF community richness

Field samples for all sites, excluding pine forests, contained similar numbers of AMF species and/or morphospecies based on the diversity of spores isolated from field samples and trap cultures (Table 3). The majority of species detected from spores belonged to genera *Acaulospora* Gerd. & Trappe emend. Berch and *Glomus* Tulasne & Tulasne. These genera contributed 21 species each to the 61 total species detected. The remaining 19 species belonged to the genera *Pacispora* Oehl & E. Sieverd., *Gigaspora* Gerd. & Trappe, *Scutellospora* Walker & Sanders, *Archaeospora* Morton & Redecker and *Entrophospora* Ames & Schneider. *Acaulospora delicata*, *A. mellea*, *A. scrobiculata* and *Glomus clarum* were recovered from all mature forest sites. Sorensen's Quotient of Similarity for mature forest sites ranged from 51% for Bazom and Tzontehuitz, 24% for Bazom and Veracruz and 36% for Tzontehuitz and Veracruz. Several morphospecies were detected in both indigenous soil and multispore trap cultures for which no published species description adequately fit.

During a single sampling period, 35 AMF species were found in soil samples from La Cascada. These included 13 species in burned areas and 29 in mature forest areas but the site was slashed and burned during the course of the study making only one sampling date possible.

A total of 26 AMF species were detected within Bazom and surrounding pine forests (Table 3). Twenty-two AMF species of these were found in milpas, 19 in mature forests and 2 in the pine forests. Milpa and mature forest AMF generic richness was high (Table 3) but no spores in the genus *Gigaspora* were found in mature forests. Species similarity between these sites was also high (Sorensen's Quotient of Similarity 83%). However, there was no overlap in AMF morphospecies isolated from trap cultures between milpas and mature forests (Table 3). Cultures from mature forest soil only produced two species in the genus *Acaulospora*, whereas cultures of milpa soil produced eight AMF species in six genera. Pine forests contained only a few spores within the genus *Glomus* and no spores were detected in trap cultures (Table 3).

Thirty-four AMF species were detected in Tzontehuitz, Chiapas (Table 3). These included 22 in burned areas, 14 in logged areas (selectively logged) and 28 species in the mature forest areas. Disturbance types had similar numbers of species in the genera *Acaulospora* and *Entrophospora* (Table 3). Richness of species in the genus *Glomus* was lowest in logged areas. Arbuscular mycorrhizal spore richness in logged areas was 74 and 59% similar to burned areas and mature forests, respectively. Mature forest and burned areas were 69% similar (Sorensen's Quotient of Similarity). Species richness in the genera *Gigaspora* and *Scutellospora* were greatest in mature forest soils (Table 3). In multispore trap cultures, seven AMF species sporulated in soils from mature forest and burned areas, whereas only four species sporulated in trap cultures started with soil from logged areas (Table 3).

In Huatusco, Veracruz, forest and pastures, 29 AMF species were detected from field samples (Table 3). Similar numbers of AMF species were found in pasture areas (21 species) and mature forest (25 species). For mature forest and pasture areas, Sorensen's Quotient of Similarity was 69% for field estimates of richness. AMF generic richness was high and, also, similar for the two disturbance types (Table 3). Likewise, multispore

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

Table 3
Occurrence of arbuscular mycorrhizal species from three areas that varied by disturbance

	Bazom sites[a]			Tzontehuitz sites[b]			Veracruz sites[c]	
	Milpa	Mature forest	Pine forest	Burned areas	Selectively logged areas	Mature forests	Mature Forests	Pasture
Acaulospora colossica				a	a	a		
Acaulospora delicata	a	a		a	a	a	a, b	a, b
Acaulospora denticulate				a	a	a, b	a, b	a, b
Acausospora elegans							a	a
Acaulospora foveata							a	
Acaulospora lacunosa		a						
Acaulospora laevis	a, b	a	a	a, b	a, b	a, b		
Acaulospora mellea	a	a, b		a, b	a, b	a, b	a	a
Acaulospora morrowiae		a	a		a			
Acaulospora myriocarpa								a
Acaulospora nicolsonii								b
Acaulospora rehmii							a	
Acaulospora scrobiculata	a	a, b		a	a	a	a, b	
Acaulospora spinosa	a	a		a	a		a, b	a
Acaulospora undulata					a, b	a		
Acaulospora sp.	a	a		b		b	a	b
Acaulospora sp. 1				a				
Acaulospora sp. 2				a	a	a		
Acaulospora sp. 3								
Acaulospora sp. 4				a		a		
Archaeospora leptoticha	a	a		b	a		b	a
Entrophospora colombiana					a			
Entrophospora infrequens	a, b							
Entrophospora schenckii	a, b	a						
Entrophospora sp.				a	a	a	a	a
Gigaspora gigantea	a, b			a	a	a	a	a
Gigaspora margarita	a				a	a	a, b	
Ggaspora rosea						a	a	
Gigaspora sp.					a			
Glomus claroideum							a	a
Glomus clarum	a	a				a	a, b	a
Glomus heterosporum					a	a		a
Glomus hoi	a	a		a	b	a		
Glomus lacteum								a, b
Glomus multicaule							a	
Glomus melanosporum	a			a			a	a
Glomus mosseae	a, b	a						
Glomus radiatum			a					
Glomus rubriformis	a	a		a	a	a		a
Glomus sinuosum	a	a		a	a	a		
Glomus spuricum							a	
Glomus tortuosum							a	
Glomus sp. 1	a	a				a		
Glomus sp. 2				a		a		
Glomus sp. 3				a				
Glomus sp. 4						a		
Glomus sp. 5	a, b	a		b		a	a	a, b
Pacispora scintillans		a		a, b		a		
Scutellospora calospora	a, b					a		a, b
Scutellospora erythropa							a	
Scutellospora fulgida	a, b	a					a, b	a, b
Scutellospora pellucida	a					a		
Scutellospora scutata						a	a	
Scutellospora verrucosa						a	a	a
Scutellospora sp. 1						a		
Scutellospora sp. 2						a		
Total species[d]	22(8)	19(2)	2(0)	20(7)	14(4)	28(7)	25(7)	21(6)

Occurrence was based on spore presence in soil samples collected three times during the course of a year (a). ($n = 18$ samples per site, where each sample is a composite of four soil samples collected in a 4 m^2 area three times throughout the course of 1 year.) Species detected in multispore trap cultures for five samples from each of the three sites after 6 months of culture (b).

[a] Sorensen's Quotient of Similarity for milpa and mature forest sites is 83%.

[b] Sorensen's Quotient of Similarity: 74% (burned areas and logged areas); 59% (logged areas and mature forest) and 69% (burned areas and mature forest).

[c] Sorensen's Quotient of Similarity: 69%.

[d] Total species followed by number of species in trap culture in parentheses.

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

trap cultures produced similar numbers of AMF species (Table 3). For mature forest soils, seven AMF species sporulated. Six species sporulated in soils from each of the two pasture areas (Table 3).

3.2. Seasonal differences in AMF sporulation across disturbance types

AMF sporulation (mean number of spores per g soil per sample) was significantly affected by season at the Bazom and Veracruz sites (Table 4). Significantly, contrasting seasonal patterns of AMF sporulation were detected across disturbance types in Bazom (Fig. 2). In mature forests, sporulation was significantly higher in the fall than in the summer and winter. Otherwise, spore numbers were consistently low in pine-dominated forests and did not differ among seasons in milpas (Fig. 2). Significant effects of seasons on AMF sporulation at the Veracruz site were attributed to significantly lower sporulation during summer relative to both the dry and rainy seasons. However, within Tzontehuitz, no differences in sporulation among seasons or disturbance types were detected for plant communities (Table 4).

Seasonal effects significantly impacted AMF species richness for the Bazom and Veracruz sites (Table 4). Overall effects of disturbance type significantly impacted AMF species richness in Bazom plant communities. As with AMF sporulation, very low means for AMF richness in pine forests were a source of the significant effects of disturbance type and season on richness (Fig. 3a). However, AMF richness in milpas was significantly higher than in mature forest. For mature forest sites and milpas, AMF spore richness was significantly higher in the fall and summer than in the winter. At the Veracruz site, overall AMF species richness was lowest in the summer relative to other seasons and highest during the rainy season (all seasons significantly differed from one another by Tukey–Kramer HSD: $P < 0.05$). In both the Bazom ejido and in Tzontehuitz, disturbance type and season interacted to significantly affect AMF species richness (Table 4). In Bazom, these contrasting seasonal patterns across disturbance types can be partly attributed to high summer AMF richness means in milpas relative to high fall means in mature forests. Similarly, in Tzontehuitz, burned areas had higher means for AMF species richness in summer where summer means for mature forests were lowest (Fig. 3b).

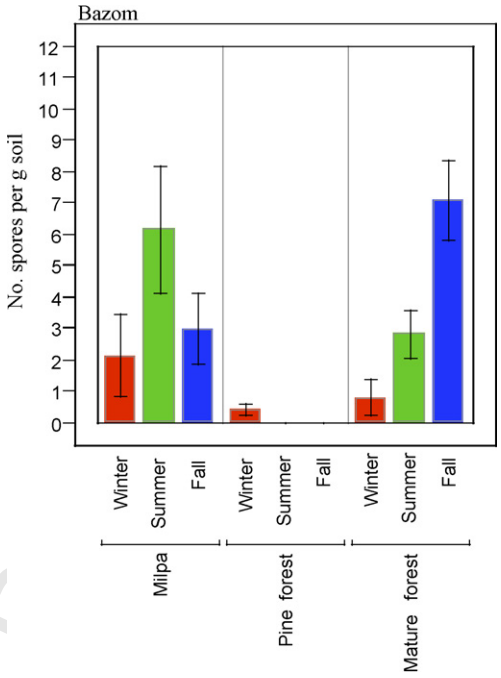

Fig. 2. Seasonal patterns of arbuscular mycorrhizal fungal sporulation for three sites in a Mexican montane rainforests (Tzontehuitz, Chiapas). Number of spores per g soil for each disturbance type and season in which samples were collected ($n = 6$ where soil was sub-sampled from a composite of four 50 cm^3 samples collected from a 4 m^2 area). Error bars are ±1S.E.M.

The disturbance × season interaction significantly affected AMF familial patterns of sporulation in Bazom and in Veracruz (Table 4), but not in Tzontehuitz (Table 5). In Bazom, sporulation for the family Gigasporaceae was significantly higher in milpas than in mature forest or pine forest areas (Fig. 4a). Otherwise family level sporulation did not differ between mature forests and milpas. In milpas, sporulation for Gigasporaceae peaked in summer whereas Archaeosporaceae sporulation was only detectable in fall. Sporulation rates for both families were significantly higher than those in winter. In mature forests, Glomeraceae and Acaulosporaceae sporulation was significantly higher in fall than in winter. Pine forest sporulation for all families was consistently low (for all

Table 4
Effects of season and disturbance type on arbuscular mycorrhizal sporulation (spores/g) and species richness at three sites in Mexican montane rainforests

	Spore number (g)			Species richness		
	Bazom	Tzontehuits	CRUO-Veracruz	Bazom	Tzontehuits	CRUO-Veracruz
Model	6.45****	1.41	5.95***	28.94****	3.07**	26.95****
Disturbance	11.67****	NS	0.07	65.89****	2.96	1.54
Season	4.06*	NS	12.49****	24.29****	1.75	66.17****
Disturbance × season	4.98**	NS	2.34	12.79****	3.78**	0.43
R^2 (%)	53.73	NS	49.79	83.73	35.27	81.79

F ratios, P values and total percentage of variance explained (R^2) in a standard least squares fit model. Number of spores/g soil was calculated for each sample ($n = 6$ where each sample was a composite of four soil samples). Richness is the mean number of species detected for each composite soil sample (soil was sub-sampled from a composite of four 50 cm^3 samples and scores were adjusted to reflect the number of species detected in a 10 g soil sample), sampling period (season) and disturbance type. *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; ****$P \leq 0.0001$.

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

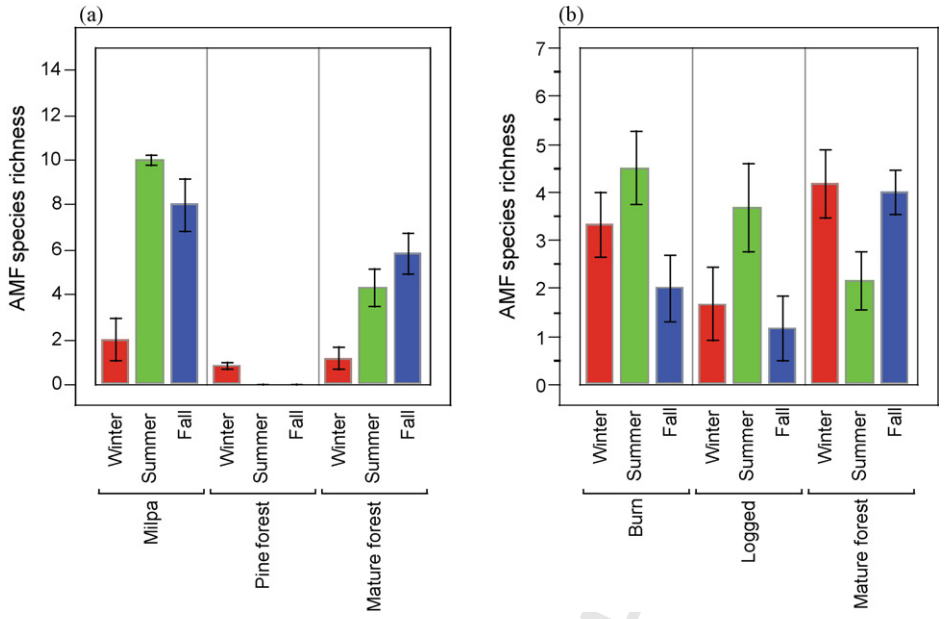

Fig. 3. Seasonal patterns of mean spore richness for arbuscular mycorrhizal fungal (AMF) species for two Mexican montane rainforests and adjacent disturbed sites. Sites are in the ejidos (a) Bazom (Chiapis) and (b) Tzontehuitz (Chiapas). Richness is the mean number of species detected for each 10 g soil sample (sub-sampled from a composite of four 50 cm^3 samples collected from a 4 m^2 area), sampling period (season) and disturbance type ($n = 6$). Error bars are ±1S.E.M.

pairwise comparisons significance was determined using Tukey–Kramer HSD: $P < 0.05$).

In Tzontehuitz, disturbance type and season were important to predicting AMF family sporulation (Table 5). Spores in Gigasporaceae were detected most frequently in mature forests but spore numbers for these families were low (Fig. 4b). Post hoc comparisons for Glomeraceae sporulation across disturbance types revealed no differences (sporulation for this family was highly variable) but Acaulosporaceae sporulation was significantly higher in burned area than in logged areas (Tukey's HSD: $P < 0.05$). In burned areas, Acaulosporaceae sporulation was high in both winter and summer but consistently low in logged areas (Fig. 4b).

In Veracruz, seasonal patterns of AMF family sporulation were more complicated. Season alone was important to predicting AMF family sporulation and patterns of AMF family sporulation contrasted across disturbance types (Table 5). Patterns of sporulation were similar to the other sites in that, as in milpas and burned areas, in pastures most AMF taxa sporulated during different seasons relative to mature forests (Fig. 4c). Seasonal patterns of sporulation did not significantly differ between mature forests and pastures for Acaulosporaceae (Fig. 4c). In mature forests, sporulation peaked in the dry season for Glomeraceae and Gigasporaceae but in the rainy season for Acaulosporaceae, whereas in pastures sporulation for these same families all peaked during the rainy season (Fig. 4c).

3.3. Soil glomalin concentrations

No differences in soil glomalin concentrations in the top 10 cm of soil among transects were found within any site

Table 5
Results of MANOVA examining the effects of disturbance and season on sporulation for the arbuscular mycorrhizal fungal families: Gigasporaceae, Archaeosporaceae, Acaulosporaceae and Glomaceae

Terms	Numerator df	Denominator df	Wilks' λ	*F*
Relatively undisturbed mature forests, selectively logged pine forests and milpas (diverse cornfields) within and surrounding (Basam ejido in Chiapas)				
Disturbance type	10	82	0.086	19.70****
Season	10	82	0.180	11.12****
Disturbance type × season	20	136.93	0.103	6.73****
Relatively undisturbed mature forests, selectively logged forests and burned areas (Tzontehuits, Chiapas)				
Disturbance type	8	84	0.615	2.89**
Season	8	84	0.694	2.11*
Disturbance type × season	16	128.95	0.619	1.37
Relatively undisturbed mature forests and pastures (diverse grasslands) within (CRUO, Veracruz)				
Disturbance type	4	27	0.081651	0.55
Season	8	54	0.476107	3.03**
Disturbance type × season	8	54	0.552248	2.33*

*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; ****$P \leq 0.0001$.

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

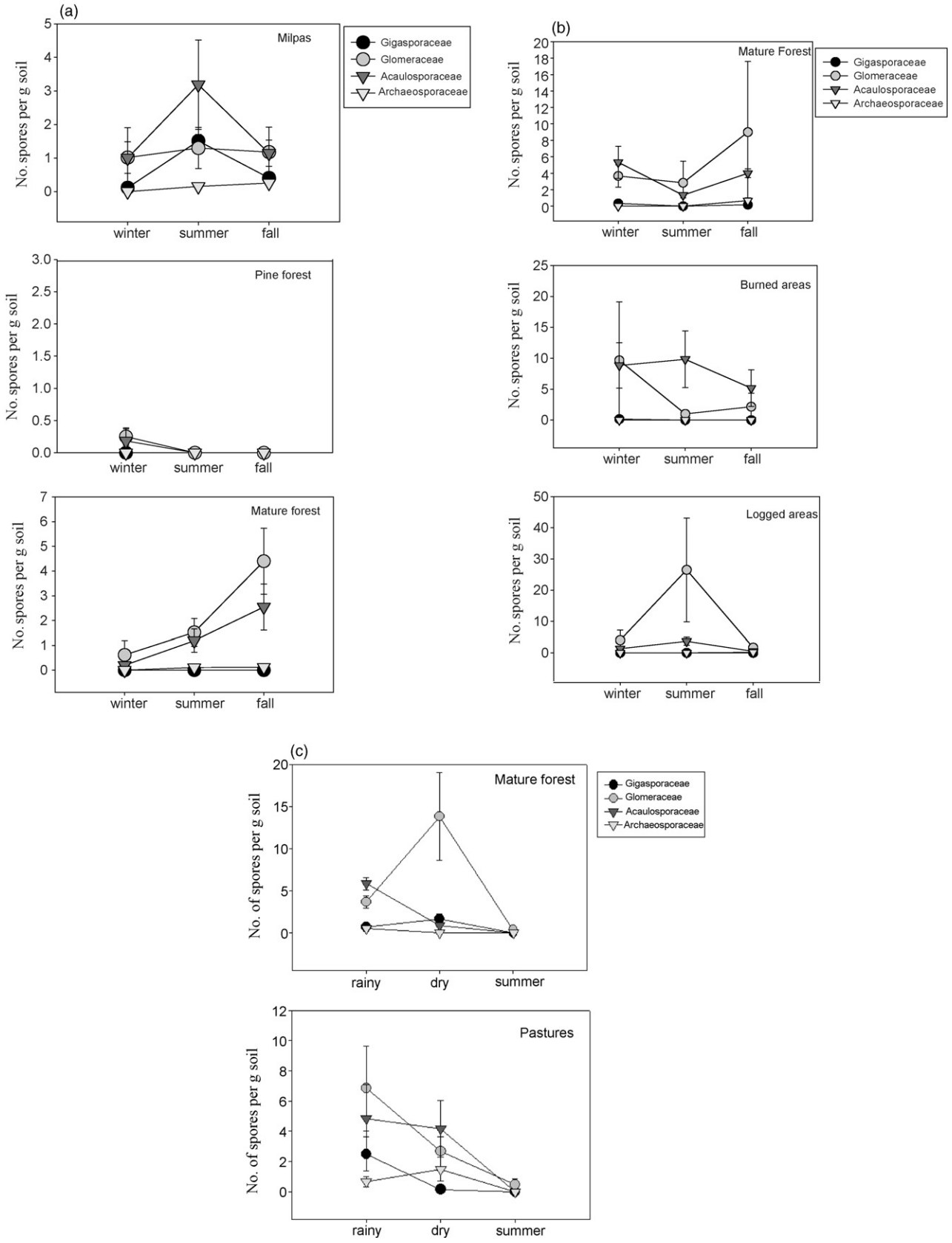

Fig. 4. Seasonal patterns of arbuscular mycorrhizal fungal sporulation by family (Gigasporaceae, Archaeosporaceae, Acaulosporaceae and Glomaceae) for different disturbance types in (a) Bazom (Chiapas), (b) Tzontehuitz (Chiapas) and (c) Centro Regional Universitario Oriente (CRUO), Veracruz. Seasonal differences existed between Veracruz (semitropical) and Chiapas (temperate). Accordingly, Veracruz seasons are labeled "rainy" (September), dry (early February) and rainy (early July). Number of spores per g soil for each disturbance type and season in which samples were collected ($n = 6$, where each sample was sub-sampled from a composite of four 50 cm^3 samples collected from a 4 m^2 area). Error bars are ±1S.E.M.

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

Table 6
Means for soil glomalin (MAb32B11 immunoreactive protein mg g^{-1} soil)

Disturbance type								Mean glomalin (mg g^{-1} soil)
tz-mature forest	A							12.24 (2.903)
tz-burn	A	B						11.51 (2.282)
lc-mature forest		B	C					7.93 (0.757)
tz-log		B	C					6.35 (0.651)
lc-burn			C					4.55 (0.395)
oc/mi-pine forest				D				3.11 (0.207)
c-pine forest				D	E			3.30 (0.705)
sjf-pine forest				D	E	F		2.58 (0.245)
ba-mature forest					E	F	G	1.91 (0.660)
ba-milpa						F	G	1.53 (0.970)
ba-milpa2							G	1.04 (0.237)

Standard errors of the means are given in parentheses. Initial test was an ANOVA ($F_{10, 517} = 49.98$; $P < 0.0001$). Pairwise comparisons (Tukey–Kramer HSD) for all disturbance types at all sites in Chiapas are shown. Sites (tz = Tzontehuits, lc = La Cascada, oc/mi, c, sjf and ba are all sites in or near the Bazom ejido) and disturbance types [mature forest, burned area (burn), non-selectively logged area (log), pine forests (which were selectively logged) and milpa] were based on site history (last 10 years) and plant composition. Levels not connected by same letter are significantly different ($P < 0.05$).

($P > 0.05$) but there were significant differences between the two milpas, two pastures and several pine forests sampled. For this reason, each pasture, milpa and pine forest included in the study was treated separately. In Chiapas, significant differences in glomalin concentrations (mg g^{-1} soil) were detected across all sites (Table 6) and between the mature forests and adjacent disturbed areas (Fig. 5). The highest concentrations of glomalin were found in soils from mature forests and burned areas at Tzontehuitz (Table 6). Although higher than any sites within the Bazom site, La Cascada mature forests had mean soil glomalin concentrations that were significantly lower than those of the mature forest of Tzontehuitz, but not the burned areas of Tzontehuitz. Burned areas in La Cascada also had significantly higher soil glomalin concentrations than any areas located in Bazom, but they did not differ from those in adjacent La Cascada mature forests. Lowest values were detected for Bazom milpas and mature forests (Table 6).

Disturbance significantly affected soil glomalin concentrations at the local scale at all sites (Fig. 5a–d). Disturbance appeared to significantly change soil glomalin concentrations in the Bazom area (ANOVA results glomalin: $F = 6.47$, $P = 0.002$). Mature forest conversion to pine-dominant forests did not appear to impact soil glomalin concentration. Only one of the two milpas had significantly lower mean glomalin concentrations than mature forest and both milpas tested had significantly lower soil glomalin values than any of the three pine-dominant forests (Fig. 5b). Test results (ANOVA) for Tzontehuitz (glomalin: $F = 31.61$, $P < 0.0001$), La Cascada (glomalin: $t = -3.33$, $P = 0.001$) and Veracruz (glomalin: $F = 65.81$, $P < 0.0001$) showed that disturbance can significantly and negatively impact soil glomalin concentration. However, at Tzontehuitz, burning did not appear to negatively impact glomalin concentrations relative to mature forests but logging was associated with lower soil glomalin means (Fig. 5c). At La Cascada and Veracruz, the significant effects of disturbance could be explained by a reduced concentration of soil glomalin in disturbed areas relative to those of mature forests (Fig. 5a and d). For example, in La Cascada, burned areas had a significantly lower concentration of glomalin relative to mature forests (Fig. 5a). Results were the same for Veracruz pastures and mature forests, where pastures had lower mean soil glomalin concentrations relative to mature forest areas (Fig. 5d).

4. Discussion

4.1. Spatio-temporal differences in AMF sporulation, species richness and composition

Measures of AMF spore richness, total sporulation and/or composition implied that overall the AMF community was not negatively impacted by mature forest conversion to milpa, pasture, burned or logged shrublands/herbaceous plant communities. Excluding mature forest conversion to pine, disturbance alone did not negatively impact AMF composition on the familial level or overall AMF spore richness (as detected by intensive sampling of AMF spores throughout a year). Instead, conversion to milpa resulted in higher AMF spore richness and no impact on total AMF sporulation. Across the sites included in this study, there appears to be high probability that the majority of AMF present were detected since our AMF morphospecies richness estimates are at the high end of the range of estimates based on rDNA sequences for temperate, montane cloud and tropical forests. Estimates based on rDNA sequences for these forest communities are between 5 and 29 AMF taxa and between 2 and 28 for the sites within our study (Husband et al., 2002; Vandenkoornhuyse et al., 2002; Opik et al., 2006).

Although we found no evidence of a reduction in AMF richness or changes in AMF composition following most disturbances, contrasting seasonal patterns of AMF spore richness and/or composition were detected among forests and adjacent disturbed areas. At the family level, AMF phenologies varied and individual family phenology sometimes differed between mature forests and adjacent disturbed areas. Data from trap cultures provided further support that infectivity of different AMF taxa differed seasonally between mature forests and adjacent disturbed areas. The number of AMF

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

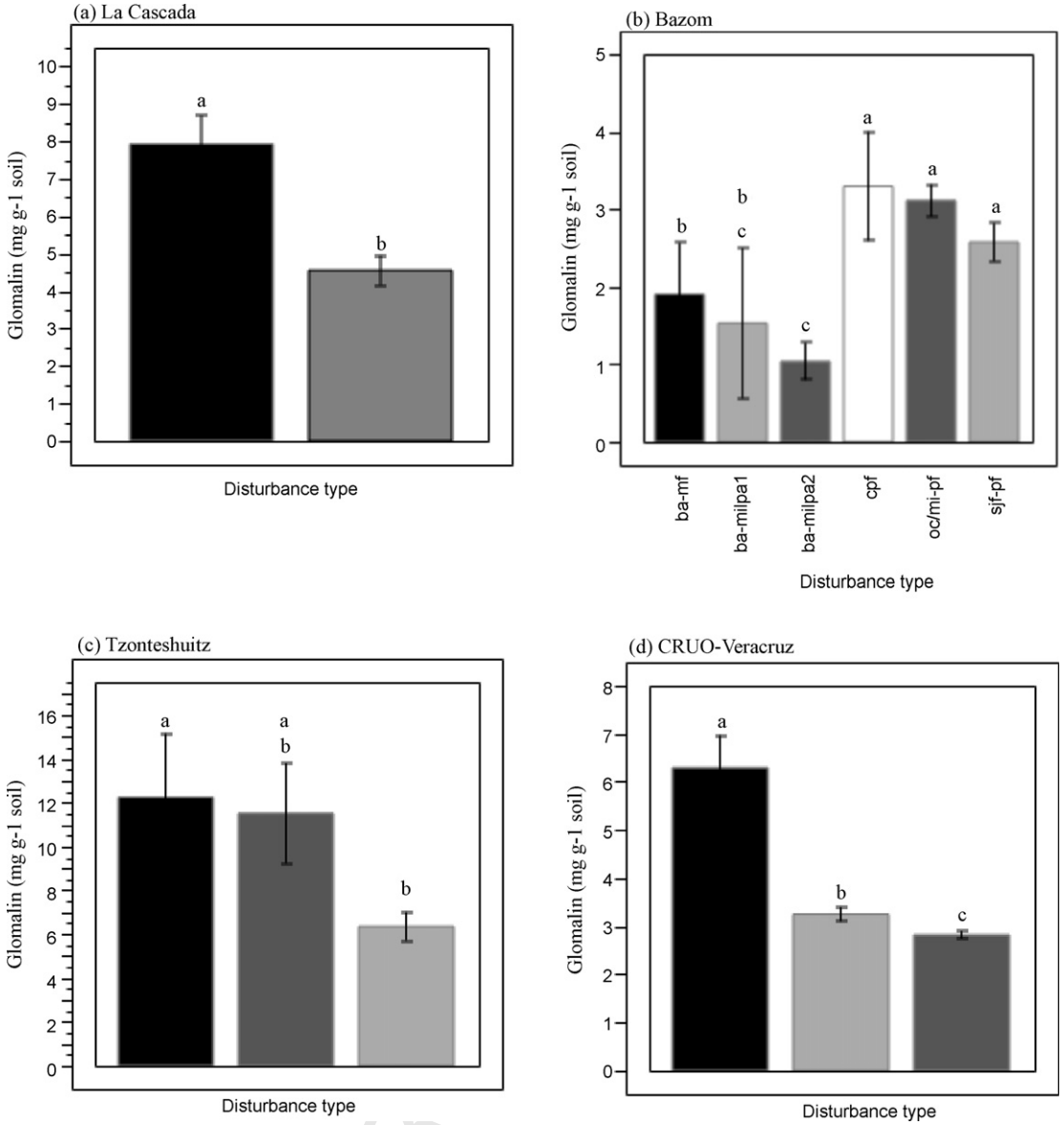

Fig. 5. Effect of different disturbances on soil glomalin (quantified with monoclonal antibody MAb32Bl1 in an enzyme-linked immunosorbent assay; Wright and Upadhyaya, 1996) expressed in mg g^{-1} soil. (a) Disturbance types are mature forests (ba-mf), pine forests (c-pf, sjf-pf and oc/mi-pf) and milpas (ba-milpa and ba-milpa2) in the Bazom ejido, Chiapas. (b) Disturbance types are mature forests (mf), burned areas (burn) and logged areas (log) in Tzontehuits, Chiapas. (c) Disturbance types are burned areas (burn) and mature forests (mf) in La Cascada, Chiapas. (d) Disturbance types are pastures (pasture-cafe and pasture-agri) and mature forests (mf) in Centro Regional Universitario Oriente (CRUO), Veracruz. Comparisons for all pairs were performed using Tukey–Kramer HSD. Bars not connected by same letter are significantly different ($P < 0.05$). Error bars are ±1S.E.M.

morphospecies detected in trap cultures approximated the number detected in any one season and similarity indices between mature forests and adjacent disturbed areas were generally lower for trap cultures than for overall richness estimates.

Mature forest conversion to pine-dominated forest clearly reduced AMF spore density. The most obvious explanation is that AMF community was negatively impacted by a shift in host plant community composition towards dominance by non-AM plant species. Among North American mixed conifer, pine forest and aspen forests, AMF infectivity did not vary (Fisher and Fule, 2004). However, this finding may have been due to the existence of understory AM plants. In the pine-dominated stands in this study, the forest understory was generally free of vegetation or had low understory fern cover.

The finding that no AMF family level changes, or changes to overall AMF morphospecies composition, existed between most disturbance types is not in total agreement with previous studies. In our study, conversion from mature forest to milpa increased Gigasporaceae sporulation and conversion to pasture did not appear to have a negative effect on this family. Further, total AMF spore species richness for multispore trap cultures was higher for soils collected from milpas relative to adjacent mature forests. This strongly contrasts with findings from tropical areas that state species within Gigasporaceae were absent or lower in spore number in both severely disturbed and

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

revegetated sites (Cuenca et al., 1998; Allen et al., 2003). It should be noted that estimates for AMF spore richness in Cuenca et al. (1998) were based on only one sampling period, whereas the study described herein based estimates on three sampling periods within distinct seasons and on trap cultures. The idea of large-spored, ''late seral'', Gigasporaceae and small-spored, ''early-seral'', disturbance-adapted Glomeraceae, as proposed by Allen et al. (2003), can clearly be rejected for Mexican montane communities.

Our results were particularly significant because milpa conversion can be considered a severe disturbance due to long fallow periods (>2 months) and dramatic changes to the plant community. Other types of severe disturbances, such as soil erosion, greatly reduced AMF spore numbers (Khan, 1978; Day et al., 1987). However, in several other studies, AMF spore diversity was relatively unaffected or slightly improved following disturbances (Abbott and Robson, 1991; Johnson et al., 1991; Picone, 2000). As in our study, other studies have demonstrated that where conversions of forests to pasture was accompanied by a shift from a mixed AM and EM forest community to that of a AM plant-dominated grassland, some aspects of AMF species diversity were altered, but overall AMF diversity was improved (Johnson and Wedin, 1997; Picone, 2000). In a Veracruz tropical rainforest, small-scale, low intensity disturbances (gap effects) had no impact on AMF community composition (Guadarrama and Alvarez-Sanchez, 1999). These studies taken together imply that the composition of the post-disturbance plant community, and not disturbance severity, best predicts AMF resilience.

Several studies provide data that help to explain the dynamic and resilient nature of the AMF community observed in our study. It is well known that different patterns of AMF spore production occur within the rhizosphere of different but coexisting plant species (Sanders and Fitter, 1992; Bever et al., 1996). Also, the AMF species that occupy the roots of conspecific plants can differ depending upon the abiotic conditions under which the plant is growing, and possibly upon the species of neighboring plants (Haas and Menge, 1990; Helgason et al., 1999). A logical extension of these findings is that different mature forests should have had great AMF morphospecies overlap and similar AMF phenology, whereas different patterns of spore production and a more disparate AMF community would be found in adjacent disturbed areas. Such patterns were found for more similar AMF communities (based on the presence of AMF spores) of geographically distant mainland tropical forest fragments relative to those of the mainland sites and closer-proximity islands (Mangan et al., 2004). The similarity among distant forest fragments was hypothesized attributable to forest fragment size. However, Mangan et al. (2004) noted that the single sampling period upon which these relationships depended did not account for possible seasonal effects on AMF sporulation. In our study, contrasting patterns of AMF taxa sporulation were indeed documented among mature forests and adjacent disturbed areas, but disturbed areas were more similar in AMF morphospecies composition (determined by the presence of spores detected in samples collected three times during the course of a year and in trap cultures) to adjacent mature forests than mature forests were to one another.

There were some AMF family level similarities among mature forest sites in our study. Patterns of sporulation for the dominant taxa, Acaulosporaceae and Glomeraceae, and maximum overall morphospecies richness were similar among mature forests (fall). Similar peaks in AMF sporulation and morphospecies richness more commonly occurred in the summer for disturbed areas. This temporal variation in the AMF community reinforces long-suspected links between host plant phenology and maintenance of AMF diversity (Bever et al., 1996, 2001; Pringle and Bever, 2002). Studies ranging from a Veracruz tropical rainforest (Guadarrama and Alvarez-Sanchez, 1999) to a North Carolina grassland (Pringle and Bever, 2002) documented contrasting seasonal patterns of sporulation among different AMF taxa (Moutoglis et al., 1995; Guadarrama and Alvarez-Sanchez, 1999; Pringle and Bever, 2002).

Across the Mexican montane sites in this study, high AMF morphospecies similarity and contrasting patterns of sporulation for individual AMF taxa were observed between mature forests and adjacent disturbed areas with very different host plant communities. Thus, not only may ''temporal niche partitioning'' be important to the maintenance of AMF diversity, as proposed by Pringle and Bever (2002), but AMF seasonal patterns in sporulation may ''reassemble'' or ''shift'' in response to changes to host plant community composition such that individual AMF taxa sporulate in different seasons. In our study sites these contrasting patterns of AMF sporulation for individual taxa among mature forests and disturbed areas provided an explanation of how AMF diversity is maintained following dramatic changes to the host plant community. Thus, it seems plausible that Mangan et al. (2004) were not observing a convergence of AMF communities but possibly a convergence of AMF taxa seasonalities in forest fragments of similar size and tree species composition.

The mechanism that drives changes to AMF community phenology post-disturbance is unknown but may be tied to phenological differences among the plants. It has long been established that root exudates regulate the AM symbiosis (Schwab et al., 1991) and that plants vary in the quantity and composition of carbohydrates (Schwab et al., 1983) and nutrients (Paynel et al., 2001) they exude into the rhizosphere according to host plant phenology, taxa, and the environmental conditions under which the host is growing (Lynch and Whipps, 1990). Different AMF may have different carbon and nutrient requirements for sporulation and this may explain differing AMF phenologies. Bever et al. (1996) determined that grassland host plants could drive differences as to when different AMF taxa sporulated. However, An et al. (1993) demonstrated that phenologically distinct host plants did not produce different patterns of AMF sporulation. Thus, the basis for AMF phenological differences may not be simply attributable to differences in individual host plant phenology but probably complex community-level AMF–plant interactions. In summary, our study demonstrates that seasonal patterns of sporulation for AMF taxa were more likely to be

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

altered by disturbance than overall AMF spore richness, composition or number where a diverse assemblage of host plants remain.

4.2. Effect of disturbance on soil glomalin concentrations

Concentrations of glomalin in soils from the forests in Chiapas (means for individual sites ranged from 1.04 to 12.24 mg g^{-1} soil) and Veracruz (means for individual sites ranged from 2.85 to 6.45 mg g^{-1} soil) are consistent with those published for temperate forests and tropical rainforests. In temperate forests, glomalin ranged between 2 and 15 mg g^{-1} soil, Hawaiian soils had up to 60 mg g^{-1} soil (Rillig et al., 2001) and Costa Rican rainforest estimates were 3.94 mg cm^{-3} soil (Lovelock et al., 2004). Disturbance-related changes to soil glomalin concentrations in this study also are consistent with published accounts in the literature. Several studies have shown that soil glomalin concentrations reflect land-use change, such as conversion of forest to agricultural areas and changes in agricultural practices (Wright et al., 1999; Rillig et al., 2003). In this study, the lack of change in soil glomalin concentration found when mature forests were converted to pine-dominant forests was unexpected. Relative to other pasture and milpa conversions, burning-related reductions in soil glomalin concentrations were also low. In North American forest soils, soil glomalin concentration was also not strongly affected by fire. Instead density and diversity of herbaceous plants and N availability were significantly related to soil glomalin concentration (Knorr et al., 2003).

In pine forests, several explanations exist for the lack of reduction in soil glomalin despite severe changes to the AMF community and host plant losses. Strong effects of the historic mature forest community (which included AM plant species), slow decomposition rates for glomalin and the low soil disturbance associated with the non-mechanized selective logging operations used at these sites are possible explanations for the high soil glomalin concentrations in pine-dominated stands.

4.3. Disturbance-related changes to AMF sporulation and glomalin pools in soils

New data indicate that MAb32B11 immunoreactive glycoprotein is produced by an AMF heat shock protein gene (Gadkar and Rillig, 2006). In many fungi, sporulation can be triggered by reductions in the availability of carbohydrates or specific nutrients (Moorelandecker, 1983) and AMF stress is known to induce AMF sporulation (Mosse, 1973). A high number of AMF taxa sporulating post-disturbance may indicate that the AMF community is under stress. Further study is needed to determine if AMF in early-successional communities are often under stress and if this facilitates the establishment of better soil conditions via rapid glomalin production.

Overall, these results show soil disturbance more strongly impacted glomalin concentrations but not the AMF community. Whereas the AMF community was strongly negatively affected by conversion of mature forests to pine-dominated forests, short-term negative effects on soil glomalin concentrations were not detected. Shifting temporal niche partitioning may explain how AMF community diversity is maintained following dramatic changes in the host plant community. The basis for temporal niche partitioning appears to be due to the great phenological plasticity of individual AMF taxa that allows them to coexist in sites with different abiotic conditions (e.g. soil type, microclimate, etc.) and host plant communities.

5. Synthesis and applications

Results are encouraging in that AMF communities in these ecosystems appear remarkably resilient and AMF function may be restored quickly, or perhaps is not lost, following common land-use changes (i.e., forest conversion to milpa, pasture or shrubland via burning). The lack of negative impacts on the AMF community at many sites may facilitate the restoration of high glomalin concentrations in soil. Excluding pine forests, reforestation efforts in montane forests may not need to include restoring AMF diversity to disturbed sites. Inoculation with AMF may only be necessary to promote good growth of AM trees during nursery production and to reduce transplant shock during reforestation (Menge et al., 1978). For this purpose, AMF inoculum should be produced from single, surface-sanitized AMF spores to exclude soil pathogens (Menge, 1984). Given the extreme soil degradation (including reductions in glomalin concentrations) associated with the most common disturbances and the steep slopes upon which these communities exist, future studies that test methods of managing AMF to improve soil conditions *in situ* may help to hasten montane forest restoration.

Uncited references Q5

Bethlenfalvay (1982), Bever (1999), Francis and Read (1995), Johnson et al. (1997), Peng et al. (1993), Smith and Smith (1996) and Rillig (2003).

Acknowledgments

We thank the Department of Plant Pathology of the University of California-Riverside (UCR), the Universidad Autónoma-Chapingo (UACH), Centro Regional Universitario Oriente (UACH), Memoria Fundación Salvador Sánchez Colin (CICTAMEX), the USDA-ARS-Soil Microbial Systems Lab (Beltsville) for laboratory space and equipment used in this research. The authors also thank Y. Reynosa, E. Evansky, G. Davolous, G. Klein for their technical support, K. White Migliaccio for creating the map, and D. Janos for comments on this manuscript. This work was supported by a grant from Foreign Agricultural Service of United States Department of Agriculture and a Dissertation Research Grant from the University of California Institute for Mexico and the United States awarded to HAV. Several anonymous reviewers provided helpful comments on this manuscript.

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

References

Abbott, L.K., Robson, A.D., 1991. Factors influencing the occurrence of vesicular–arbuscular mycorrhizas. Agric. Ecosyst. Environ. 35, 121–150.

Alexopoulos, C.J., Mims, C.W., Blackwell, M., 1996. Introductory Mycology, 4th ed. John Wiley & Sons Inc., New York.

Allen, E.B., Allen, M.F., Egerton-Warburton, L., Corkidi, L., Gómez-Pompa, A., 2003. Impacts of early- and late-seral mycorrhizae during restoration in seasonal tropical forest, Mexico. Ecol. Appl. 13, 1701–1717.

An, Z.Q., Guo, B.Z., Hendrix, J.W., 1993. Populations of spores and propagules of mycorrhizal fungi in relation to the life cycles of tall fescue and tobacco. Soil Biol. Biochem. 25, 813–817.

Azcón-Aguilar, C., Palenzuela, J., Roldán, A., Bautista, S., Vallejo, R., Barea, J.M., 2003. Analysis of the mycorrhizal potential in the rhizosphere of representative plant species from desertification-threatened Mediterranean shrublands. Appl. Soil Ecol. 22, 29–37.

Bethlenfalvay, G.J., 1982. Conditions affecting parasitic or mutualistic growth in mycorrhizal plants. Phytopathology 72, 950–1950.

Bever, J.D., 1999. Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. Ecol. Lett. 2, 52–62.

Bever, J.D., Morton, J.B., Antonovics, J., Schultz, P.A., 1996. Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. J. Ecol. 84, 71–82.

Bever, J.D., Schultz, P.A., Pringle, A., Morton, J.B., 2001. Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. Bioscience 51, 923–931.

Brush, S.B., Tadesse, D., Van Dusen, E., 2003. Crop diversity in peasant and industrialized agriculture: Mexico and California. Soc. Nat. Resour. 16, 123–141.

Cayuela, L., Benayas, J.M.R., Echeverria, C., 2006. Clearance and fragmentation of tropical montane forests in the Highlands of Chiapas, Mexico (1975–2000). For. Ecol. Manage. 226, 208–218.

Cuenca, G., De Andrade, Z., Escalante, G., 1998. Diversity of Glomalean spores from natural, disturbed and revegetated communities growing on nutrient-poor tropical soils. Soil Biol. Biochem. 30, 711–719.

Dalpe, Y., 1989. Ericoid mycorrhizal fungi in the Myxotrichaceae and Gymnoascaceae. New Phytol. 113, 523–527.

Day, L.D., Sylvia, D.M., Collins, M.E., 1987. Interactions among vesicular–arbuscular mycorrhizae, soil, and landscape position. Soil Sci. Soc. Am. J. 51, 635–639.

Fisher, M.A., Fule, P.Z., 2004. Changes in forest vegetation and arbuscular mycorrhizae along a steep elevation gradient in Arizona. For. Ecol. Manage. 200, 293–311.

Francis, R., Read, D.J., 1995. Mutualism and antagonism in the mycorrhizal symbiosis, with special reference to impacts on plant community structure. Can. J. Bot. 73, S1301–S1309.

Gadkar, V., Rillig, M.C., 2006. The arbuscular mycorrhizal fungal protein glomalin is a putative homolog of heat shock protein 60. FEMS Microbiol. Lett. 263, 93–101.

Graham, J.H., 2000. Assessing costs of arbuscular mycorrhizal symbiosis in agroecosystems. In: Podila, G.K., Douds, D.D. (Eds.), Current Advances in Mycorrhizae Research. American Phytopathological Society, St. Paul, MN, pp. 127–140.

Guadarrama, P., Alvarez-Sanchez, F.J., 1999. Abundance of arbuscular mycorrhizal fungi spores in different environments in a tropical rain forest, Veracruz, Mexico. Mycorrhiza 8, 267–270.

Haas, J.H., Menge, J.A., 1990. Va-mycorrhizal fungi and soil characteristics in Avocado (*Persea americana* Mill) Orchard soils. Plant Soil 127, 207–212.

Hart, M.M., Reader, R.J., Klironomos, J.N., 2001. Life-history strategies of arbuscular mycorrhizal fungi in relation to their successional dynamics. Mycologia 93, 1186–1194.

Helgason, T., Fitter, A.H., Young, J.P.W., 1999. Molecular diversity of arbuscular mycorrhizal fungi colonising *Hyacinthoides nonscripta* (bluebell) in a seminatural woodland. Mol. Ecol. 8, 659–666.

Husband, R., Herre, E.A., Turner, S.L., Gallery, R., Young, J.P.W., 2002. Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. Mol. Ecol. 11, 2669–2678.

International Humic Substances Society (IHSS), 2006. Product information (online). Available at http://www.ihss.gatech.edu/.

Jansa, J., Mozafar, A., Anken, T., Ruh, R., Sanders, I.R., Frossard, E., 2002. Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza 12, 225–234.

Jasper, D.A., Abbott, L.K., Robson, A.D., 1991. The effect of soil disturbance on vesicular arbuscular mycorrhizal fungi in soils from different vegetation types. New Phytol. 118, 471–476.

Johnson, N.C., Graham, J.H., Smith, F.A., 1997. Functioning of mycorrhizal associations along the mutualism–parasitism continuum. New Phytol. 135, 575–586.

Johnson, N.C., Wedin, D.A., 1997. Soil carbon, nutrients, and mycorrhizae during conversion of dry tropical forest to grassland. Ecol. Appl. 7, 171–182.

Johnson, N.C., Zak, D.R., Tilman, D., Pfleger, F.L., 1991. Dynamics of vesicular–arbuscular mycorrhizae during old field succession. Oecologia 86, 349–358.

Khan, A.G., 1978. Vesicular–arbuscular mycorrhizas in plants colonizing black wastes from Bituminous Coal Mining in Illawarra Region of New South Wales. New Phytol. 81, 53–63.

Knorr, M.A., Boerner, R.E.J., Rillig, M.C., 2003. Glomalin content of forest soils in relation to fire frequency and landscape position. Mycorrhiza 13, 205–210.

Law, R., 1985. Evolution in a mutualistic environment. In: Boucher, D.H. (Ed.), The Biology of Mutualism. Oxford University Press, New York, pp. 29–39.

Lovelock, C.E., Wright, S.F., Clark, D.A., Ruess, R.W., 2004. Soil stocks of glomalin produced by arbuscular mycorrhizal fungi across a tropical rain forest landscape. J. Ecol. 92, 278–287.

Lynch, J.M., Whipps, J.M., 1990. Substrate flow in the rhizosphere. Plant Soil 129, 1–10.

Mangan, S.A., Eom, A.H., Adler, G.H., Yavitt, J.B., Herre, E.A., 2004. Diversity of arbuscular mycorrhizal fungi across a fragmented forest in Panama: insular spore communities differ from mainland communities. Oecologia 141, 687–700.

Menge, J.A., Davis, R.M., Johnson, E.L.V., Zentmyer, G.A., 1978. Mycorrhizal fungi increase growth and reduce transplant injury in Avocado. Calif. Agric. 32, 6–7.

Menge, J.A., 1984. Inoculum production. In: Powell, C.L., Bagyaraj, D.J. (Eds.), VA Mycorrhiza. CRC Press Inc., Boca Raton, FL, pp. 187–203.

Mera-Ovando, L.M., 1989. Condiciones naturales para la producción. In: Parra-Vázquez, M.R. (Ed.), El Subdesarrollo Agrícola en Los Altos de Chiapas. Universidad Autónoma Chapingo, Chapingo, pp. 21–82.

Montiel, R.B., Robledo, M.J.D., 1998. Caracterización, Descripción y Evaluación de Especies Frutales en el Banco Genético del CRUO. Universidad Veracruzana, Córdoba, Veracruz, México.

Moorelandecker, E., 1983. Fundamentals of the Fungi, 2nd ed. Prentice Hall, NJ.

Morton, J.B., 1990. Evolutionary relationships among arbuscular mycorrhizal fungi in the endogonaceae. Mycologia 82, 192–207.

Morton, J.B., Bentivenga, S.P., Bever, J.D., 1995. Discovery, measurement, and interpretation of diversity in arbuscular endomycorrhizal fungi (Glomales, Zygomycetes). Can. J. Bot.: Rev. Can. Bot. 73, S25–S32.

Mosse, B., 1973. Advances in the study of vesicular–arbuscular mycorrhiza. Annu. Rev. Phytopathol. 11, 171–196.

Moutoglis, P., Klironomos, J., Widden, P., Kendrick, B., 1995. Direct observation of spores of vesicular–arbuscular mycorrhizal fungi growing on Sugar Maple roots in the field, using sodium hexametaphosphate as a soil dispersant. Mycologia 87, 419–423.

Muniz-Castro, M.A., Williams-Linera, G., Benayas, J.M.R., 2006. Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. J. Trop. Ecol. 22, 431–440.

Nichols, K.A., Wright, S.F., 2006. Carbon and nitrogen in operationally defined soil organic matter pools. Biol. Fertil. Soils 43, 215–220.

Ochoa-Gaona, S., González-Espinosa, M., 2000. Land use and deforestation in the highlands of Chiapas, Mexico. Appl. Geogr. 20, 17–42.

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016

Olsson, P.A., Thingstrup, I., Jakobsen, I., Bååth, F., 1999. Estimation of the biomass of arbuscular mycorrhizal fungi in a linseed field. Soil Biol. Biochem. 31, 1879–1887.

Opik, M., Moora, M., Liira, J., Zobel, M., 2006. Composition of root-colonizing arbuscular mycorrhizal fungal communities in different ecosystems around the globe. J. Ecol. 94, 778–790.

Pawlowska, T.E., 2005. Genetic processes in arbuscular mycorrhizal fungi. FEMS Microbiol. Lett. 251, 185–192.

Paynel, F., Murray, P.J., Cliquet, J.B., 2001. Root exudates: a pathway for short-term N transfer from clover and ryegrass. Plant Soil 229, 235–243.

Peng, S.B., Eissenstat, D.M., Graham, J.H., Williams, K., Hodge, N.C., 1993. Growth depression in mycorrhizal citrus at high-phosphorus supply—analysis of carbon costs. Plant Physiol. 101, 1063–1071.

Picone, C., 2000. Diversity and abundance of arbuscular-mycorrhizal fungus spores in tropical forest and pasture. Biotropica 32, 734–750.

Pringle, A., Bever, J.D., 2002. Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in a North Carolina grassland. Am. J. Bot. 89, 1439–1446.

Ramirez-Marcial, N., 2003. Survival and growth of tree seedlings in anthropogenically disturbed Mexican montane rain forests. J. Veg. Sci. 14, 881–890.

Ramirez-Marcial, N., González-Espinosa, M., Williams-Linera, G., 2001. Anthropogenic disturbance and tree diversity in montane rain forest in Chiapas, Mexico. For. Ecol. Manage. 154, 311–326.

Redecker, D., Kodner, R., Graham, L.E., 2000. Glomalean fungi from the Ordovician. Science 289, 1920–1921.

Rillig, M.C., 2003. Arbuscular mycorrhizae, glomalin, and soil aggregation. Can. J. Soil Sci. 84, 355–363.

Rillig, M.C., 2004. Arbuscular mycorrhizae and terrestrial ecosystem processes. Ecol. Lett. 7, 740–754.

Rillig, M.C., Mummey, D.L., 2006. Mycorrhizas and soil structure. New Phytol. 171, 41–53.

Rillig, M.C., Ramsey, P.W., Morris, S., Paul, E.A., 2003. Glomalin, an arbuscular-mycorrhizal fungal soil protein, responds to land-use change. Plant Soil 253, 293–299.

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 Soil 233, 167–177.

Rosier, C.L., Hoye, A.T., Rillig, M.C., 2006. Glomalin-related soil protein: assessment of current detection and quantification tools. Soil Biol. Biochem. 38, 2205–2211.

Rzedowski, J., 1978. Vegetación de México. Editorial Limusa, Mexico City.

Sanders, I.R., Fitter, A.H., 1992. Evidence for differential responses between host fungus combinations of vesicular arbuscular mycorrhizas from a grassland. Mycol. Res. 96, 415–419.

Schenck, N.C., Perez, Y., 1990. Manual for the Identification of VA Mycorrhizal Fungi, 3rd ed. Synergistic Publications, Gainesville, FL.

Schwab, S.M., Menge, J.A., Leonard, R.T., 1983. Quantitative and qualitative effects of phosphorus on extracts and exudates of sudangrass roots in relation to vesicular–arbuscular mycorrhiza formation. Plant Physiol. 73, 761–765.

Schwab, S.M., Menge, J.A., Tinker, P.B., 1991. Regulation of nutrient transfer between host and fungus in vesicular arbuscular mycorrhizas. New Phytol. 117, 387–398.

Smith, F.A., Smith, S.E., 1996. Mutualism and parasitism: diversity in function and structure in the ''arbuscular'' (VA) mycorrhizal symbiosis. In: Callow, J.A. (Ed.), Advances in Botanical Research, vol. 22. pp. 1–43.

Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis, 2nd ed. Academic Press, London, UK.

Stahl, P.D., Williams, S.E., Christensen, M., 1988. Efficacy of native vesicular arbuscular mycorrhizal fungi after severe soil disturbance. New Phytol. 110, 347–354.

Steinberg, P.D., Rillig, M.C., 2003. Differential decomposition of arbuscular mycorrhizal fungal hyphae and glomalin. Soil Biol. Biochem. 35, 191–194.

Tacher, S.I.L., Rivera, J.R.A., Romero, M.M.M., Fernandez, A.D., 2002. Characterization of the traditional use of spontaneous flora in the Lacanha Lacandonian community, Chiapas, Mexico. Interciencia 27, 512–520.

Urcelay, C., Díaz, S., 2003. The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity. Ecol. Lett. 6, 388–391.

Vandenkoornhuyse, P., Husband, R., Daniell, T.J., Watson, I.J., Duck, J.M., Fitter, A.H., Young, J.P.W., 2002. Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. Mol. Ecol. 11, 1555–1564.

Wright, S.F., Anderson, R.L., 2000. Aggregate stability and glomalin in alternative crop rotations for the central Great Plains. Biol. Fertil. Soils 31, 249–253.

Wright, S.F., FrankeSnyder, M., Morton, J.B., Upadhyaya, A., 1996. Time-course study and partial characterization of a protein on hyphae of arbuscular mycorrhizal fungi during active colonization of roots. Plant Soil 181, 193–203.

Wright, S.F., Starr, J.L., Paltineanu, I.C., 1999. Changes in aggregate stability and concentration of glomalin during tillage management transition. Soil Sci. Soc. Am. J. 63, 1825–1829.

Wright, S.F., Upadhyaya, A., 1996. Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. Soil Sci. 161, 575–586.

Wright, S.F., Upadhyaya, A., 1998. A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. Plant Soil 198, 97–107.

Wright, S.F., Upadhyaya, A., 1999. Quantification of arbuscular mycorrhizal fungi activity by the glomalin concentration on hyphal traps. Mycorrhiza 8, 283–285.

Zuill, H.A., Lathrop, E.W., 1975. The structure and climate of a tropical montane rain forest and an associated temperate Pine–Oak–Liquidambar forest in the northern highlands of Chiapas, Mexico. Ann. Instit. Biol. UNAM Ser. Bot. 46, 73–118.

Please cite this article in press as: Violi, H.A., et al., Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico, Forest Ecol. Manage. (2007), doi:10.1016/j.foreco.2007.08.016