

Research Article

Heterogeneity in mycorrhizal inoculum potential of flood-deposited sediments

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Abstract. Riparian areas are diverse systems where flooding creates new sites for establishment of vegetation. Symbioses with soil microorganisms, such as mycorrhizal fungi, affect vascular plant growth and community composition. It is unknown, however, how mycorrhizal fungi are dispersed along rivers and what potential they have to inoculate roots of plants establishing on recently deposited sedimentary surfaces of flood plains. We measured AMF inocula in sediment deposited by an average spring flood along an expansive riverine flood plain in Montana, USA, to determine whether AMF inocula

were present in sediments and what types of propagules (spores, hyphae, or colonized root fragments) contribute to AMF infectivity. Flood-deposited sediments contained sufficient inocula for AMF to colonize host plants (*Sorghum sudanense*) grown in a greenhouse, and both AMF hyphal lengths and spore densities were correlated with infectivity. Availability of mycorrhizal inocula, which is patchily distributed in this system, may lead to microsites that differ in ability to support establishment and growth of early-successional plants.

Key words. Arbuscular mycorrhiza; flood; mycorrhizal inoculum potential; river.

Introduction

Most vascular plants form symbioses with mycorrhizal fungi that associate with roots and provide nutrients to their hosts in exchange for carbohydrates (Allen, 1991; Chapin et al., 2002; Smith and Read, 2008). These fungi influence a range of functions, including uptake of nutrients that often benefit plant growth (Smith and Read, 2008), protection of roots from pathogens and soil-dwelling herbivores (e.g. Boro-

wicz, 2001; Newsham et al., 1995), aggregation of soil and subsequent carbon storage (Rillig, 2004; Rillig and Mummey, 2006), and enhancement of plant diversity (van der Heijden et al., 1998). Although mycorrhizal fungi have been studied extensively in upland ecosystems, much less is understood about their ecology at aquatic-terrestrial transitional areas of rivers and streams known as riparia (Naiman et al., 2005). Arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (ECMF) occur in riparian areas (Jacobson, 2004; Beauchamp et al., 2006, 2007; Piotrowski et al., 2008). Some riparian plants, notably *Populus* species, which are ubiquitous in temperate

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and subarctic riparia, form associations with both AMF and ECMF (Lodge, 1989; Jacobson, 2004). Benefits to plant growth mediated by AMF have been documented in a riparian context. A non-native herbaceous plant that colonizes North American flood plains, spotted knapweed (*Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek, following Ochsman (2001); also known as *C. maculosa* in North American literature), achieved > 400% increase in growth relative to non-mycorrhizal plants when grown with AMF in recently deposited floodplain sediments (Harner et al., unpublished data).

Propagules of mycorrhizal fungi exist as spores, pieces of extraradical hyphae (ERH), and colonized root fragments (Klironomos and Hart, 2002). In upland systems, propagules are distributed by animals, especially small mammals (Warner et al., 1987; Mangan and Adler, 2000), earthworms and ants (Harinikumar and Bagyaraj, 1994), as well as wind (Allen, 1987; Warner et al., 1987; Allen et al., 1989). In contrast, little is known about AMF ecology in relation to soil and plant succession in riparia. AMF occur in soil in early years of vegetation colonization following floods (Piotrowski et al., 2008; Harner et al., unpublished data). However, types of fungal propagules that may colonize sediments deposited by floods and spatial variability in fungal inocula at early-successional sites are unknown. Dispersal of seeds by water (hydrochory) is a primary mechanism for establishment of plants on flood plains (Andersson et al., 2000; Jansson et al., 2005; Merritt and Wohl, 2006). An analogous process may distribute propagules of mycorrhizal fungi to early-successional riparian sites, thereby establishing symbioses that enhance primary succession.

Our study was motivated by the probability that mycorrhizal fungi mediate growth and survival of pioneer seedlings, thus influencing primary succession in floodplain landscapes. Our objective was to describe variability in AMF inocula in sediments deposited by an average spring flood on an expansive riverine flood plain. Specifically, we measured mycorrhizal inoculum potential and abundance of infectious propagules (spores, hyphae, and colonized root fragments) in newly deposited sediments not yet colonized by vascular plants. Characterization of this variation is important because spatial heterogeneity in mycorrhizal inoculum potential may lead to microsites with varying capacities to support growth and survival of pioneer seedlings (e.g. Gange et al., 1993; Lovelock and Miller, 2002), and thus alter dynamics of plant establishment and succession in these dynamic landscapes.

Materials and methods

Study site

The study was conducted at the Nyack Flood Plain (48° 26' 30" N, 113° 48' 12" W) of the Middle Fork of the Flathead River (freely flowing, 5th order, catchment area of 2300 km²) in northwestern Montana, USA. At Nyack, the river has a mean annual flow of 82 m³ s⁻¹, an average peak annual discharge of 541 m³ s⁻¹ associated with spring snowmelt, and an average base flow of 17 m³ s⁻¹ typically reached in fall or early winter (Whited et al., 2007). The flood plain is 10-km long by 3-km wide and located about 20 km upstream from West Glacier, Flathead County, Montana, on the southern boundary of Glacier National Park. Nyack is a site of long-term research focusing on ecosystem dynamics occurring within the habitat mosaics of a large floodplain system (Stanford et al., 2005). Gravel and sand bars are redistributed annually in actively flooded areas, and patches of regenerative vegetation comprised of cottonwood trees, willows and other shrubs, and herbaceous plants are common. On less frequently flooded benches, mature cottonwoods and conifers occur as later successional forests (Mouw and Alaback, 2003). Across the riparian chronosequence at Nyack, abundance of AMF increases in early successional vegetation (< 13 years after plant establishment), while ECMF abundance increases continuously as forests mature (Piotrowski et al., 2008).

Sample collection and sediment characterization

We sampled open sediment surfaces on gravel bars one month after a spring flood (342 m³ s⁻¹ on 4 June 2005; Fig. 1). We selected four sites (each ~ 25 m²; Fig. 2), where we visually determined floods had deposited fresh sediment, rather than scoured existing sediments. These flood-deposited sediments may have been transported to the sampling sites over some distance or reworked locally. We sampled at the earliest possible time post-flood, when flood waters had receded from and allowed access to sites. Sites were adjacent to the main river channel, not yet colonized by plants, and located at varying distances from existing stands of vegetation. Site 3 was < 10 m and other sites were > 50 m away from patches of vegetation (Fig. 2). Sediment samples were collected from four random locations per site with a trowel to a depth of 10 cm. Sampling to 10 cm maintained consistency of methods with previous mycorrhizal surveys on the flood plain (Piotrowski et al. 2008a), as well as ensured that only newly deposited materials were sampled.

We transported samples to the laboratory within 24 h and transferred subsamples immediately to pots for assays of mycorrhizal inoculum potential (see

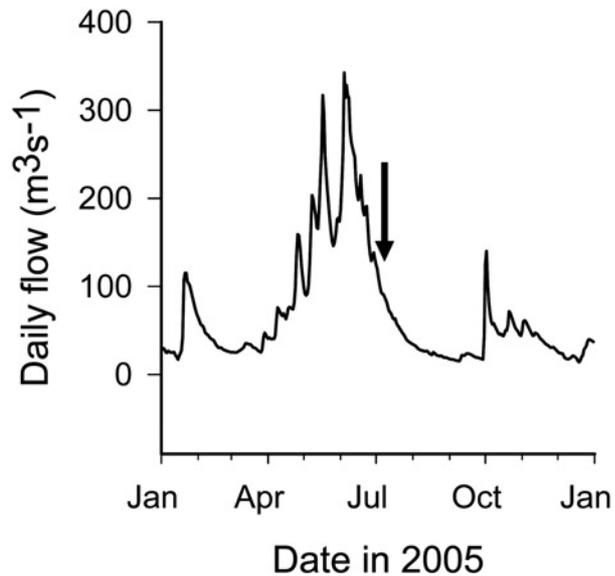


Fig. 1. Average daily discharge in the Middle Fork of the Flathead River measured by USGS gage 12358500 near West Glacier, Montana, in 2005. Arrow denotes when sediments were collected from Nyack Flood Plain during recession of the spring spate.

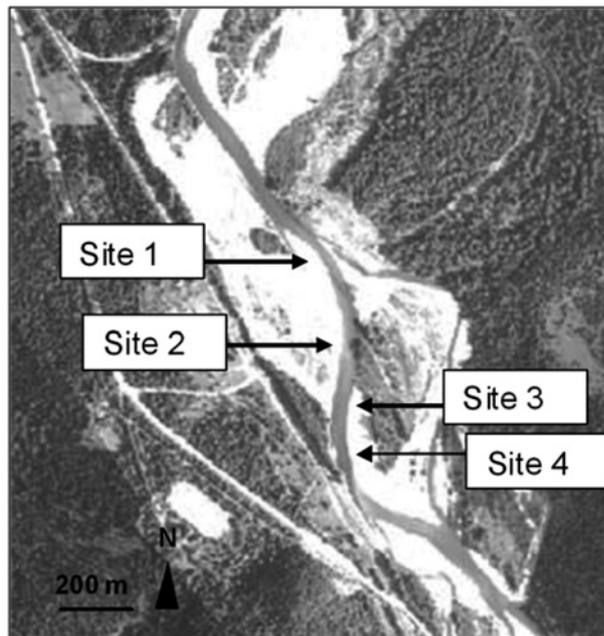


Fig. 2. Location where sediments were collected adjacent to the main channel of the Middle Fork of the Flathead River on the upstream portion of Nyack Flood Plain. River flows from southeast to northwest.

following section). The remainder of each sample was air-dried for subsequent analyses of spore densities, extraradical hyphal (ERH) lengths, and root fragments (see following section), as well as for physical and chemical characteristics. Sediments were analyzed for particle size (% sand, silt, and clay), pH,

organic matter content (% OM), bioavailable nutrients [nitrate-nitrogen (NO_3^- -N), Olsen phosphorus (Olsen-P), and potassium (K)], and soluble salts at the Soil Testing Laboratory at South Dakota State University in Brookings, South Dakota, USA. Only two subsamples had enough material remaining for chemical analyses at site 3.

Mycorrhizal measurements

Mycorrhizal inoculum potential (MIP) is an integrative measure of infective fungal propagules present in soil and is estimated using a plant-growth bioassay (e.g. Koide and Mooney, 1987; Boerner et al., 1996). In a MIP assay, the initial density of fungal propagules is proportional to the amount of fungal colonization of host roots, as long as there are no secondary infection units in roots. Therefore, plants are harvested after a relatively short time to avoid counting secondary infection units. Spores, hyphae, and roots are all components of the MIP (Klironomos and Hart, 2002), but their individual contributions to infectivity cannot be distinguished by the assay. Therefore, individual components of MIP are measured separately with direct methods. Direct methods, however, do not indicate whether the respective propagule type is infective. Combined, MIP assays and direct methods provide complementary measures of abundance and infectivity of AMF propagules in soils/sediments.

To estimate MIP, we added 100 ml of field-collected sediment to 115 ml pots (Cone-Tainers™, Stuwe and Sons, Inc., Canby, OR, USA). Each pot received three seeds of *Sorghum sudanense* that were thinned to two plants per pot after germination. Plants were grown in a greenhouse for 30 days, watered with tap water as needed, and harvested. We stained fungal structures in roots with trypan blue as described by Brundrett et al. (1994) and mounted root segments on slides. We scored ~ 50 root intersections per sample for mycorrhizal colonization at magnification of 200× on a Nikon Eclipse E600 microscope following a modification of the magnified intersections method described by McGonigle et al. (1990). MIP was quantified as percentage of intersections containing any AMF structures (AMF hyphae, vesicles, or arbuscles). AMF hyphae were distinguished from other fungal hyphae as described in Rillig et al. (1998).

For direct measurements of potential fungal propagules, we measured ERH lengths, spore densities, and inspected samples for root fragments. To determine ERH lengths, hyphae were extracted from 4 g subsamples by an aqueous extraction and membrane filter technique (Rillig et al., 1999). AMF spores were extracted from 50 ml of soil by the sucrose centrifugation technique (Brundrett et al., 1994), separated into diameter size classes (38–106 μm, 106–250 μm,

Table 1. Physical and chemical characteristics of flood-deposited sediments at four sites adjacent to the active river channel.

Site	% Sand	% Silt	% Clay	pH	% OM	NO ₃ ⁻ -N (mg kg ⁻¹)	Olsen-P (mg kg ⁻¹)	K (mg kg ⁻¹)	Soluble salts (µS cm ⁻¹)
1	86.0 (3.3)	1.0 (0)	13.0 (3.3)	8.1 (0.1)	0.4 (0.1)	13.0 (3.7)	4.0 (0.6)	29.5 (2.3)	350 (150)
2	93.8 (0.5)	1.0 (0)	5.3 (0.5)	8.4 (0.0)	0.1 (0.0)	9.4 (3.4)	2.8 (0.3)	19.0 (0.7)	150 (29)
3	85.5 (3.8)	9.8 (5.7)	4.8 (2.0)	8.4 (0.0)	0.3 (0.1)	4.8 (0.8)	3.0 (0.0)	23.0 (1.0)	100 (0)
4	93.5 (0.6)	1.0 (0)	5.5 (0.6)	8.4 (0.0)	0.1 (0.0)	5.6 (0.6)	2.8 (0.3)	20.5 (0.5)	100 (0)

Notes: Values are means (1 SE) for $n = 4$, except $n = 2$ for site 3 nutrient measures. Differences among sites were detected for % sand, pH, % OM, K, and soluble salts ($P < 0.05$; Kruskal-Wallis test).

and $> 250 \mu\text{m}$), and counted under a stereomicroscope. We searched sediments for root fragments visible without magnification.

Data analysis

Nonparametric Kruskal-Wallis tests were used to test the null hypothesis that soil characteristics (texture, pH, % OM, NO₃⁻-N, Olsen-P, K, or soluble salts) and AMF parameters (MIP, ERH lengths, and spore densities) did not differ among sites. We also assessed correlations between AMF parameters and soil characteristics across sites with a Pearson test. Test results were considered significant at $P < 0.05$ and marginally significant at $P < 0.10$. Statistical analyses were performed with SPSS version 12.0 for Windows (Chicago, Illinois, USA).

Results

Sediments deposited by the flood were coarse, mostly sand or loamy sand, alkaline, and had low availability of nutrients (Table 1). Average MIP, determined as the percentage AMF root infection of *Sorghum sudanense*, ranged from 0–39% across all subsamples and differed among sites ($\chi^2 = 8.815$, $df = 3$, $P = 0.032$; Fig. 3a). Densities of AMF spores ranged from 0.1–1.6 spores ml⁻¹ sediment across all subsamples and differed among sites ($\chi^2 = 12.89$, $df = 3$, $P = 0.005$; Fig. 3b). Most spores (89%) were small (38–106 μm), and the remaining (11%) were of intermediate diameter (106–250 μm). Lengths of ERH ranged from 0–428 mm g⁻¹ sediment across all subsamples and differed marginally among the four sites ($\chi^2 = 6.72$, $df = 3$, $P = 0.081$; Fig. 3c). Visible roots were not present in samples. Site 3 tended to have greater hyphal lengths, greater spore densities, and higher MIP relative to other sites (Fig. 3). Site 3 was located closest to an existing stand of vegetation and contained more silt (10%) than other sites (1% silt).

MIP was correlated positively with AMF spore densities ($r = 0.973$, $P = 0.027$, $n = 4$) and ERH lengths ($r = 0.998$, $P = 0.002$, $n = 4$). ERH lengths and AMF spore densities also were correlated positively ($r =$

0.957 , $P = 0.043$, $n = 4$). Significant correlations were detected between percent silt and MIP ($r = 0.964$, $P = 0.036$, $n = 4$), as well as percent silt and ERH lengths ($r = 0.971$, $P = 0.029$, $n = 4$), but relationships were leveraged by high silt content at site 3. We did not detect other significant correlations among fungal and abiotic variables (pH, % OM, NO₃⁻-N, Olsen-P, K, or soluble salts), even though some of these variables differed across sites (Table 1).

Discussion

Our survey found viable propagules of AMF present in freshly deposited sediments along river banks following a spring flood. Abundance of propagules was low in relation to many upland habitats (Smith and Read, 2008), as might be expected after a disturbance like flooding and absence of host plants. The flood-deposited sediments contained mostly small spores (38–106 μm) and hyphae, and their abundance was correlated positively with MIP. We observed no root fragments in sediments, suggesting this additional source of inocula was of limited importance at these sampling sites. Although we did not detect root fragments, this finding does not preclude the possibility that roots serve as inocula at other sites where larger materials are redistributed and deposited. Because not all species of AMF colonize roots from the same types of propagules (Klironomos and Hart, 2002) and spore sizes differ among species (Bever et al., 2001), presence of small spores and hyphae may indicate that dispersal associated with average floods selects for specific AMF, such as *Glomus* species, in early successional sites.

Although we had a small sample size of only four sites, our results suggest a possible link between distribution of fungal propagules and fluvial transport of fine sediments that warrants consideration in future studies of plant and microbial colonization of early-successional floodplain surfaces. Because AMF spores are of similar size to silt and small sand particles, there may be selective-sorting of materials that results in co-deposition of fungal propagules and fine sediments. Additionally, smaller-sized particles offer greater surface area for attachment of propagules, especially

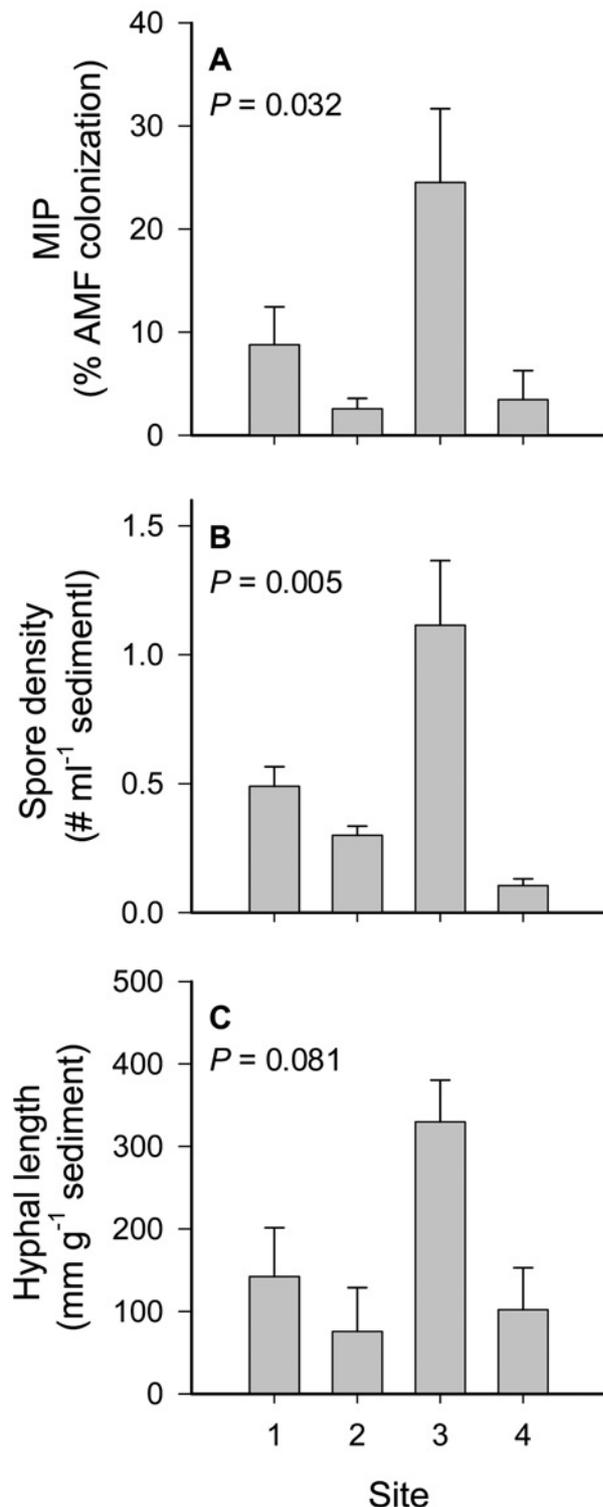


Fig. 3. Mycorrhizal inoculum potential (MIP) based on *Sorghum* bioassay (A), AMF spore density (B), and extraradical hyphal length (C) across four sites with recent sediment deposits from flooding. Bars represent mean + 1 SE for 4 replicates per site for AMF colonization and spore densities and 3 replicates per site for hyphal lengths. Differences among sites were compared with Kruskal-Wallis tests.

hyphae, so propagules may sort with fine alluvia because they are attached to individual particles. Therefore, if AMF propagules are transported by flooding, then AMF abundance, and possibly species richness, may be greater in areas where silt is deposited compared to areas where sand or larger substrates are deposited. On Nyack Flood Plain, Mouw et al. (2009) found plant species richness increased with deposits of fine sediments that accumulated behind wood debris. AMF propagules may be more abundant and species rich in fine-sediment deposits and thus contribute to plant species richness (e.g. van der Heijden et al., 1998). Indeed, in a field study, Landis et al. (2004) observed a strong, positive correlation between numbers of plant and AMF species, both of which were correlated positively with silt, clay, and nitrogen contents of soil. Interactions between sediment texture, MIP, and plant diversity require further investigation on flood plains.

Although we know of no studies specifically of AMF dispersal by floods, our observations have precedence. Researchers have described mycorrhizal inocula in sediments eroded and deposited by overland run-off during rains in a savanna ecosystem (Veenendaal et al., 1992). Dispersal of AMF propagules also has been demonstrated for beach sand and dune soils, where AMF propagules were observed before colonization of pioneer plants (Nicolson, 1960), as well as co-dispersed with vegetative fragments of pioneer plants, likely through entrainment in ocean water (Koske and Gemma, 1990). AMF spores remain viable after immersion in sea water for at least 20 d (Koske and Gemma, 1990; Koske et al., 1996). Similar viability of AMF propagules may occur during transport in river water, but this remains to be tested. Additionally, recent research has demonstrated the importance of plant dispersal by hydrochory (Andersson et al., 2000; Goodson et al., 2003; Jansson et al., 2005), whereby viable plant propagules may be stored in the channel bed and then redistributed with sediments across flood plains during high flows (Gurnell et al., 2007, 2008a). Mimics of plant seeds have been measured in transport over 100 km (Andersson et al., 2000). Spores or hyphae entangled with fine sediment may move over similarly long-distances.

In any case, AMF propagules were present and likely precursors to primary succession at Nyack Flood Plain. We expect that most inocula were deposited by the flood, but wind or animals also may disperse propagules (Allen, 1987; Warner et al., 1987; Allen et al., 1989; Harinikumar and Bagyaraj, 1994; Mangan and Adler 2000). Wind transports fine sediment ($30 \mu\text{m} < D_{50} < 64 \mu\text{m}$) to floodplain surfaces (Gurnell et al. 2008b), and mycorrhizal inocula may be present in these sediments. Smaller sized particles,

like aeolian or fluvial silts, offer a large surface area for attachment of propagules, and their primary dispersal strategies would in turn affect AMF dispersion. Future studies could disentangle relative contributions of water, wind, and animals for dispersing AMF over varying distances on flood plains through direct measurements of propagules or of spore mimics in transport by wind and water, as well as measurements of propagules in gut contents or fecal samples of animals (Warner et al., 1987; Allen et al., 1989).

Our results show that AMF inocula are available for early-successional plants in flood deposits, but the distribution of propagules is heterogeneous among sites. Furthermore, there may be an association between abundance of AMF propagules and sediment texture, which may suggest a similarity in transport and deposition (water and possibly wind) of finer (silt) particles and mycorrhizal inocula. Studies incorporating a larger number of sites and seasonal sampling will help clarify these relationships with greater confidence. The presence and amounts of these symbionts potentially affect successional trajectories of riparian plant communities. In an early-successional upland system, Gange et al. (1993) observed that AMF influence the structure of plant communities by increasing species richness, mostly by enhancing establishment of forbs. In experimental microcosms, mycorrhizae can increase biomass of subordinate species relative to the dominant species, thus contributing to increased diversity (Grime et al., 1987). Mycorrhizae also enhance uptake of mineral nutrients and thereby allow some species to survive that would otherwise remain unproductive or eventually die out (Grime et al., 1987; Smith and Read, 2008). AMF likely have similar roles on flood plains and may help plants establish on alluvial deposits that are nutrient poor. If mycotrophic plants colonize patches where AMF propagules are present, then plants may develop faster. Patches without inocula would serve as sites for colonization by non-mycotrophic plants, thus contributing to the overall heterogeneity and diversity of riparian plant communities.

An important implication of this study is to consider how river regulation affects AMF dispersal dynamics. Many forms of river regulation reduce sediment transport and deposition. If microbial inocula that plants need are intermixed with this sediment, then they may be lost when sediments are trapped behind dams and other retentive structures. This has been investigated on the Verde River in Arizona where researchers compared vegetation, soil, and AMF between a regulated and unregulated reach (Beauchamp et al., 2007). They did not detect differences in AMF richness, community composition, or colonization between the reaches, despite variation in

plant cover and soil characteristics (Beauchamp et al., 2007). Effects of dams on dispersal of plant propagules have been tested on several rivers (Jansson et al., 2005; Merritt and Wohl, 2006). In a comparison of regulated and unregulated rivers in Sweden, researchers did not find dams acting as a barrier for dispersal, but they postulated that sources of propagules will be more local on impounded rivers (Jansson et al., 2005). Along two rivers in Colorado, USA, however, researchers found > 70% reductions in seed concentrations in the water column, as well as effects on species composition, downstream of dams (Merritt and Wohl, 2006). Such studies need to be extended to other rivers and include investigations of co-dispersal of microbial inocula and plant propagules. Concurrent establishment of microbial communities and vegetation likely contributes to the heterogeneity and diversity often observed in riparian plant communities.

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