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Just a matter of time: Fungi and roots significantly and rapidly aggregate soil over four decades along the Tagliamento River, NE Italy

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ABSTRACT

Fluvial islands are emergent landforms which form at the interface between the permanently inundated areas of the river channel and the more stable areas of the floodplain as a result of interactions between physical river processes, wood and riparian vegetation. These highly dynamical systems are ideal to study soil structure development in the short to medium term, a process in which soil biota and plants play a substantial role. We investigated soil structure development on islands along a 40 year chronosequence within a 3 km island-braided reach of the Tagliamento River, Northeastern Italy. We used several parameters to capture different aspects of the soil structure, and measured biotic (e.g., fungal and plant root parameters) and abiotic (e.g. organic carbon) factors expected to determine the structure. We estimated models relating soil structure to its determinants, and, in order to confer statistical robustness to our results, we explicitly took into account spatial autocorrelation, which is present due to the space for time substitution inherent in the study of chronosequences and may have confounded results of previous studies. We found that, despite the eroding forces from the hydrological and geomorphological dynamics to which the system is subject, all soil structure variables significantly, and in some case greatly increased with site age. We interpret this as a macroscopic proxy for the major direct and indirect binding effects exerted by root variables and extraradical hyphae of arbuscular mycorrhizal fungi (AMF). Key soil structure parameters such as percentage of water stable aggregates (WSA) can double from the time the island landform is initiated (mean WSA = 30%) to the full 40 years (mean WSA = 64%) covered by our chronosequence. The study demonstrates the fundamental role of soil biota and plant roots in aggregating soils even in a system in which intense short to medium term physical disturbances are common.

1. Introduction

Soil structure emerges from the arrangement of primary soil particles into secondary units or soil aggregates (Soil Science Society of America (2008)). Several properties and functions also emerge from the interaction between the biotic and abiotic components of the soil matrix. Soil structure is of great importance in supporting the growth of plants and soil organisms (Oades, 1984; Passioura, 1991), enhancing the resistance of soil to erosion (Diaz-Zorita et al., 2002), reducing nutrient leaching (Elliott and Coleman, 1988) and assisting carbon sequestration (Wilson et al., 2009). Soil aggregation, the process by which primary soil particles are bound and oriented together to form larger complexes, either through chemical or physical processes in the soil matrix or both (Allison, 1968; Tisdall and Oades, 1982), is a key aspect of soil structure (Tisdall and Oades, 1982; Six et al., 2000b; Diaz-Zorita et al., 2002). Tisdall and Oades (1982) suggested a hierarchical hypothesis for soil aggregate formation: aggregation takes place through the binding of clay particles forming microaggregates, which are further bound together to form macroaggregates. Regardless of the specific physico-chemical details of the mechanisms involved in aggregation, several biotic and abiotic factors determine the quality, quantity and speed of soil aggregate formation. These factors include the abundance of primary soil particle sizes (clay, silt or sand) (Allison, 1968; Tisdall and Oades, 1982),

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biological exudates (Tisdall and Oades, 1982), organo-metallic compounds and cations (Bronick and Lal, 2005), soil carbon and soil nitrogen content (Gupta and Germida, 1988; Haynes et al., 1991; Mikha and Rice, 2004), and the enmeshment of particles by fine roots and fungal hyphae (Tisdall and Oades, 1982; Rillig and Mummey, 2006). Tisdall and Oades (1982) described the temporal persistence of organic binding from transient (polysaccharides), temporary (root, hyphae and microbial cells) and persistent (humic substances) elements.

Although most studies investigating soil structure have focused on agricultural ecosystems and the agroeconomical aspects of soil structure (Elliott and Coleman, 1988; Jastrow et al., 1998; Diaz-Zorita et al., 2002), there is a growing interest in the study of soil structure dynamics in natural ecosystems, including riparian areas (Piotrowski et al., 2008; Harner et al., 2011). Studying soil structure in such ecosystems provides insights into the natural dynamics of soil structure development and might be used for management purposes in the restoration of natural or semi-natural systems.

River floodplains are areas of low lying land that are constructed by river processes and are subject to frequent fluvial disturbances through inundation, erosion and construction processes (Ward et al., 1999; Naiman et al., 2005). As a result, they are very dynamic, diverse and productive areas (Tockner and Stanford, 2002), which provide an ecotone between the upland terrestrial and river channel aquatic ecosystems (Gregory et al., 1991). Through their ecotonal nature, they display sharp gradients in environmental conditions, ecological processes and plant communities (Gregory et al., 1991). Overall, floodplains offer great opportunities to investigate the process of soil aggregation and its association with issues of applied soil ecology.

Fluvial islands develop at the interface between the permanently inundated areas of the river channel and the more stable areas of the floodplain (the riparian zone), where they may attach to and extend the floodplain through sediment accretion and island enlargement or they may be excised from the floodplain by fluvial erosion processes (Gurnell et al., 2001). Fluvial islands are particularly interesting with regard to soil aggregation because in most cases they are emergent landforms that develop and grow as a result of interactions between fluvial processes and riparian vegetation including large wood (Osterkamp, 1998; Ward et al., 1999; Gurnell et al., 2005). These 'building' islands (Gurnell et al., 2001) are formed through a successional process that, in highly disturbed, large rivers, commences with the deposition of uprooted trees on gravel bar surfaces during the falling stages of major floods. In the case of riparian Saliceae species (willows and poplars), these stranded trees rapidly produce roots and shoots, which anchor them to the gravel substrate and form a flow-resistant canopy around which finer sediment, more wood pieces and other plant propagules accumulate to form 'pioneer' islands. Pioneer islands aggrade upwards and extend laterally as they accumulate more sediment, wood and seeds, develop an increasingly large and diverse vegetation canopy, and coalesce to form 'building' and eventually large 'established' islands (Edwards et al., 1999; Kollmann et al., 1999; Gurnell et al., 2001, 2005). Mosaics of islands develop through this process of island growth and coalescence and also as a result of erosion and removal during different flood events, providing island surfaces of different age and elevation that are subject to different levels of disturbance and display different geomorphological characteristics (Gurnell et al., 2001).

Previous research on chronosequences of surfaces within the riparian zone have investigated colonization of roots by arbuscular mycorrhizal fungi (AMF) and the growth of AMF extraradical hyphae in the soil matrix, which have been shown to positively influence the development of soil aggregation (Miller and Jastrow, 1990; Bearden and Petersen, 2000; Rillig et al., 2002; Rillig and Mummey, 2006). A chronosequence study of soil development within the riparian zone of the Nyack River, Montana, USA was conducted by Piotrowski et al. (2008), and showed an increase of soil aggregates size class 1–2 mm which coincided with an increase of AMF abundance during the first 13 years of the succession. Harner et al. (2011) conducted a study on a reach of the Tagliamento River, Italy, in which they categorized island types into depositional surfaces, pioneer and established islands and showed that soil aggregates size class 1–2 mm increased with site development which correlated positively to root length colonized by AMF and also AMF hyphal length.

The present research takes advantage of the process of island initiation and growth to investigate how soils develop on island surfaces of different age, with a particular emphasis on the process of soil aggregation. Here we aimed at improving our understanding of this process (i) by investigating soil structure development in a spatially explicit way (taking into account autocorrelation); and (ii) by basing inferences on a more comprehensive set of soil structure indices for macroaggregates (diameter 0.212–4 mm) on quantitatively determined island age. The research also investigates the effect of biotic and abiotic parameters on soil structure along a well established and replicated chronosequence of islands on the Tagliamento River, Italy and also assigns importance of the various biotic and abiotic variables for explaining the different soil structure indices.

2. Methods

2.1. Research site

The research was conducted on fluvial islands of the Tagliamento River, in Northeastern Italy. The Tagliamento is the last morphologically intact Alpine river system in Europe (Müller, 1995; Ward et al., 1999), thereby providing a model ecosystem in which riparian processes can be investigated (Tockner et al., 2003). The river traverses a length of 172 km from its headwaters in the Italian Alps to its mouth in the Adriatic Sea. The river has a flashy pluvio-nival regime (mean stream discharge; Q_{mean}): 109 m^3/s, (flood flows up to 4000 m^3/s), which, during large floods, supplies the river's active, braided channel and margins with numerous newly uprooted trees that underpin island development (Ward et al., 1999).

The research was conducted within a 3 km long, island-braided, gravel bed reach of the Tagliamento River located between 79.5 and 81.5 km from the river's source (46°12′24.03″N, 12°59′40.06″E to 46°12′3.62″N, 12°58′4.82″E). The reach is elevated approximately 140 m.a.s.l., and has an active corridor up to 1 km in width that contains numerous islands at different successional stages (Kollmann et al., 1999). Geomorphic features within the reach include multiple channels, gravel bars, pools, wooded islands and in the less frequently inundated, relatively stable areas of the floodplain, extensive forest. The dominant tree species is black poplar (*Populus nigra* L.), which sprouts freely following uprooting to drive island development (Gurnell et al., 2001). However, several willow species (*Salix alba* L., *Salix daphnoides* Vill., *Salix elaeagnos* Scop., *Salix purpurea* L., *Salix triandra* L.) and alder (*Alnus incana* L.) are also abundant. Particle size distribution between different geomorphological settings (surface of established islands or floodplain, pioneer islands on gravel bar surfaces and open gravel bar surfaces) showed no significant difference (Gurnell et al., 2008).

2.2. Sampling sites

The replicated chronosequence of sites that were sampled within the study reach is shown in Fig. 1. Sites ranged from 0 to 40 years since the initiation of island formation, with site and patch