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Static and Dynamic Properties of Soil Food Web Structure in a Greenhouse Environment*[1]

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ABSTRACT

Soil food web structure is fundamental to ecosystem process and function; most studies on soil food web structure have focused on agro-ecosystems under different management practices and natural terrestrial ecosystems, but seldom on greenhouses. This study explored the static and temporal variability of soil food structure in two greenhouses of Shandong Province, North China over a two-year period. The static properties were measured directly by surveying functional group composition and a series of parameters portraying the species properties, link properties, chain properties and omnivory properties of the web, as well as indirectly through calculation of nematode indices, enrichment index (EI), structure index (SI), and channel index (CI). The dynamic variability of greenhouse soil food structure was described by the dynamics of functional groups, Bray-Curtis (BC) similarity and cluster analysis. The results showed that the greenhouse soil food web contained 14 functional groups, with microbes having the highest mean biomass, followed by protozoa. Of the three functional groups of protozoa, flagellates were the dominant group on most sampling dates, amoebae only became the dominant group during the summer, while ciliates were the least prevalent group. All nematodes were assigned into one of the four functional groups, bacterivorous, fungivorous, herbivorous and omnivorous, and the fungivorous nematodes had the lowest mean biomass. Mites were assigned into three functional groups and the omnivorous noncryptostigmatic mites were the dominant group. All the functional groups showed significant seasonal changes. The soil food web connectance was 0.15, the maximum food chain length was 5, and the average food chain length was 3.6. The profiles of the EI and SI showed that the food web was resource-depleted with minimal structure. The results of CI indicated that the bacterial decomposition pathway was the dominant pathway in the food web of the greenhouse soils studied and the results of BC similarity showed that the soil food web had higher variability and instability over time. The cluster analysis showed that the functional groups located at high trophic levels with low biomass were in a cluster, whereas those at low trophic levels with high biomass were closer. Compared with the food web structure of agroecosystem and natural terrestrial ecosystem soils, the structure of greenhouse soil food web was simple and unstable, which was likely driven by high agricultural intensification, particularly over application of fertilizers.

Key Words: Bray-Curtis similarity, functional group, mites, nematodes, protozoa

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INTRODUCTION

There are currently two frontier research areas in the field of soil ecology, the ecological linkages between aboveground and belowground biota, and the soil food web (Dong, 2007). The soil food web can be categorized into three step-up levels, the connectedness web, the energy flow web, and the functional or interaction web (Hunt *et al.*, 1987; Moore and De Ruiter, 1991; Scheu, 2002). The connectedness web graphically depicts the nutritional relationship between functional groups and the direction of material and energy transfer in soil, which is generally presented by carbon (C) and nitrogen (N) flux. However, the connectedness web does not describe the extent or magnitude of the material and energy flow. The energy flow web can estimate C and N mineralization and the contribution of functional groups to the mineralization of C and N (Berg *et al.*, 2001; Schröter *et al.*, 2003). The interaction food web further describes the effects between functional groups and is regarded as an essential tool for exploring some fundamental features of soil ecology, such as the relationship between complexity and stability (De Ruiter *et al.*, 1995; Moore *et al.*, 1996; Neutel *et al.*, 2002; Neutel *et al.*, 2007).

It is important to understand the soil food web structure because of its fundamental role in soil ecosystem processes and functions. To date, direct and indi-

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rect methods have been used to depict the structure of the soil food web. Direct methods refer to survey of the soil food structure by measuring the abundance and/or biomass of the functional groups of microbes, protozoa, nematodes, and microarthropods contained within a soil. A series of parameters have been used to portray the species properties, link properties, chain properties and omnivory properties of the web, which are not only adopted by the soil food web, but are common to all webs (Pimm *et al.*, 1991; Dunne, 2006). In contrast to direct methods, indirect methods use nematodes as a power tool to assess the structure, function and resilience of a soil food web. Ferris and his colleagues (Ferris *et al.*, 2001; Ferris, 2005) integrated the nematode colonizer-persister (cp) scaling with food sources and developed a series of nematode indices such as the enrichment index (EI), structure index (SI), basal index (BI) and channel index (CI) to assess food web enrichment and connectedness. Based on these indices, researchers have conducted studies on the suppressive service of the soil food web (Sánchez-Moreno and Ferris, 2007; Sánchez-Moreno *et al.*, 2008), and on the responses of the soil food web to cover crop quality and quantity (DuPont *et al.*, 2009), agricultural practices (Sánchez-Moreno *et al.*, 2006, 2009; Li *et al.*, 2009, 2010; Liang *et al.*, 2009; Ferris *et al.*, 2012; Zhang *et al.*, 2012), environment management (Sánchez-Moreno and Ferris, 2007) and global change (Eisenhauer *et al.*, 2012; Li *et al.*, 2012). Noticeably, these method parameters represent just the static properties of the web, and do not reflect the temporal and spatial variability in the soil food web structure. To assess the variability of the soil food web, the Bray-Curtis (BC) similarity index has been used to compare the similarity in community composition for the whole food web to parts of the food web in a Scots pine forest (Bengtsson and Berg, 2005; Berg and Bengtsson, 2007). Some ecologists (Moore *et al.*, 1990; Moore and De Ruiter, 1991) have used multivariate analysis, such as cluster analysis, canonical discriminant analysis and canonical correspondence analysis, to find patterns in the way soil functional groups interact.

Existing research on soil food web structure has focused mainly on grassland (Hunt *et al.*, 1987; Irvine *et al.*, 2006), forest (Berg *et al.*, 2001; Schröter *et al.*, 2003; Berg and Bengtsson, 2007), farmland (Brussaard *et al.*, 1990; Moore *et al.*, 1990; Moore and De Ruiter, 1991; Moore, 1994), and on the restoration of abandoned land (Holtkamp *et al.*, 2008, 2011). However, little research exists on the soil food web structure of greenhouse soils. Some scientists have investigated portions of the soil food web in greenhouses, but not all of the soil biota has been surveyed. For example, Liu *et al.* (2006) investigated the nematode communities in greenhouse soils of different ages from a suburb of Shenyang, China. Li *et al.* (2010) monitored the long-term effect of fertility management on the soil nematode community in vegetable production under greenhouse conditions.

A greenhouse is an important semi-artificial agro-ecosystem that can establish a microclimate to improve crop growth and productivity by regulating and controlling indoor illumination, soil temperature and humidity, and carbon dioxide concentration. In Shandong Province, North China, 60 299 ha were cultivated under greenhouses in 2006 (EDCAY, 2006). This large scale greenhouse production contributed to the country's highest provincial production of winter vegetables and fruits. However, little is known about greenhouse ecosystems in terms of the composition and dynamics of various soil organisms, as well as the food web structure.

Compared to natural terrestrial ecosystems and farmland, greenhouse soils undergo more intensification and higher disturbance (Li *et al.*, 2010). Therefore, it is hypothesized that the greenhouse soil food web is simple and unstable in comparison with the soil food web from natural terrestrial ecosystems and farmland. The objectives of this study were to investigate and document the structure properties of the greenhouse soil food web, and establish the reasons for soil food web structure formation of greenhouses through survey of the functional groups dynamics, connectedness and temporal variability of soil food web.

MATERIALS AND METHODS

Study site

This study was conducted at a vegetable company located in Shouguang City (39°26′–39°51′ N, 116°13′–116°43′ E), Shandong Province, North China. The company operates 30 greenhouses, of which two (Greenhouses A and B) were randomly selected for the study. The study site mean annual ambient temperature is 12.4 °C, with a minimum temperature of −18 °C in winter (January) and a maximum temperature of 38 °C in summer (July). Mean annual rainfall is 608 mm, with a frost-free period of 195 d, from the middle of April until the end of October.

Greenhouses A and B, each measuring 480 m^2 (60 m × 8 m), were established on existing farmland 10 and 12 years before the study started, respectively, and