



Soil sickness of peanuts is attributable to modifications in soil microbes induced by peanut root exudates rather than to direct allelopathy



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ABSTRACT

The quantity and quality of peanut yields are seriously compromised by consecutive monoculture in the subtropical regions of China. Root exudates, which represent a growth regulator in peanut–soil feedback processes, play a principal role in soil sickness. The growth inhibition of a species in an *in vitro* bioassay enriched with root exudates and allelochemicals is commonly viewed as evidence of an allelopathic interaction. However, for some of these putative examples of allelopathy, the results have not been verified in more natural settings with plants continuously growing in soil. In this study, the phenolic acids in peanut root exudates, their retention characteristics in an Udic Ferrosol, and their effects on rhizosphere soil microbial communities and peanut seedling growth were studied. Phenolic acids from peanut root exudates were quickly metabolized by soil microorganisms and did not accumulate to high levels. The peanut root exudates selectively inhibited or stimulated certain communal bacterial and fungal species, with decreases in the relative abundance of the bacterial taxa *Gelria glutamica*, *Mitsuaria chitosanitabida*, and *Burkholderia soli* and the fungal taxa *Mortierella* sp. and *Geminibasidium hirsutum* and increases in the relative abundance of the bacterial taxon *Desulfotomaculum ruminis* and the fungal taxa *Fusarium oxysporum*, *Bionectria ochroleuca* and *Phoma macrostoma*. The experimental application of phenolic acids to non-sterile and sterile soil revealed that the poor performance of the peanut plants was attributed to changes in the soil microbial communities promoted by phenolic acids. These results suggest that pathogenic fungal accumulation at the expense of such beneficial microorganisms as plant growth promoting rhizobacteria, mycorrhizal fungi induced by root exudates, rather than direct auto-toxicity induced by root exudates, might represent the principal cause underlying the soil sickness associated with peanut plants. We hope that our study will motivate researchers to integrate the role of soil microbial communities in allelopathic research, such that their observed significance in soil sickness during continuous monocropping of fields can be further explored.

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1. Introduction

Plant–soil feedback responses, the net effects of all positive and negative interactions between plant and soil organisms, have garnered increasing attention as the underlying mechanism of several ecological phenomena, such as plant invasion, old-field

succession, and soil sickness (Kaur et al., 2009; Bever et al., 2010; van de Voorde et al., 2012). Soil sickness is an example of typical negative plant–soil feedback that results in reductions in the quantity and quality of crop yields when the same crop or its related species are cultivated successively on the same soil (Huang et al., 2013). At present, soil sickness has become a prevalent problem in the production of many annual crops that are subject to intensive monocropping, and it also affects trees and shrubs in orchards and tea plantations, where it causes replanting and regeneration problems (Canals et al., 2005). Accordingly, understanding the mechanisms underlying plant–soil feedback in

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agroecosystems is necessary to provide insights about soil sickness, as well as its solution, and for the establishment of sustainable agroecosystems.

Root exudation includes the secretion of a diverse array of carbon-containing primary metabolites, such as sugars, amino acids and phenolic acids, as well as more complex secondary compounds that are involved in plant defense and stimulatory or inhibitory interactions with other soil organisms (Bertin et al., 2003; Jones et al., 2004; Bais et al., 2006). Soil microorganisms are crucial for the sustainability and function of soil-based ecosystems because of their involvement in key processes, such as mineral nutrition cycling, organic matter turnover, soil structure formation and toxin removal (van Elsas et al., 2006; Brussaard et al., 2007). Root exudates are considered as one of the most important factors that affect soil microorganisms (Bais et al., 2006; Yao and Allen, 2006). In continuous monocropping systems, crop roots repeatedly release the same types of exudates for many years, occasionally resulting in significant colonization and infection by certain beneficial or pathogenic microorganisms that utilize these substrates. Thus, root exudates that persist during the planting season of a monoculture crop could be responsible for soil sickness, and their allelopathy should be better understood in terms of soil microbial ecology (Inderjit, 2005; Kaur et al., 2009).

Root exudates from many crops have been shown to exhibit the potential for autotoxicity (Huang et al., 2013). The phenolic acids that are present in root exudates are often considered putative allelochemicals (Kato-Noguchi and Macias, 2005; Zhou and Wu, 2012). Previous studies regarding these allelochemicals in crops, such as cucumber and soybean, have shown that these compounds can inhibit plant growth by affecting plant metabolic processes, such as photosynthesis, respiration, and ion uptake (Yu et al., 2003; Zhang et al., 2010). However, studies on the allelopathic effects of plant root exudates and their allelochemical constituents have only focused on their *in vitro* effects, excluding the involvement of microbial components. Furthermore, those studies used high concentrations of root exudates containing active allelochemicals. However, the even highest levels of these compounds detected in samples of soil previously subjected to continuous cropping were significantly below previously reported limits that would elicit biological activities and allelopathic potential (Blair et al., 2006; Perry et al., 2007). Therefore, it is unlikely that allelochemicals secreted by plant roots can accumulate within the soil to levels sufficient to exhibit biological activities that would impact plant growth.

Microbial metabolism represents an important factor for determining the magnitude and duration of allelopathic interactions attributed to phytotoxic phenolic acids present in soil (Blum, 1998; Perry et al., 2007; Cipollini et al., 2012). Many studies have shown that allelochemicals or autotoxins are easily degraded by microbes (Kaur et al., 2009; Weidenhamer et al., 2013). Blum et al. (2000) previously reported that several benzoic and cinnamic acids, which were initially present in the Cecil Ap horizon soil samples examined, became undetectable few days after amending the soil. Thus, the effects of a vast diversity of microorganisms on the fate of plant phenolic compounds (and other potential allelochemicals) found within the soil should not be underestimated (Kaur et al., 2009; Ehlers, 2011).

Recently, research studies have addressed the effects of phenolic acids, such as coumaric and vanillic acids, on soil microbial communities (Qu and Wang, 2008), and have shown that their addition can affect soil microbial populations (Zhou and Wu, 2012). However, limited information is available regarding on how gradual amendments of real root exudates affect the microbial profiles of natural soil. The autotoxicity of plant root exudates and phenolic acids on plant growth were previously thought to directly result

from their effects *in vitro*, which contributed to soil sickness. However, the pathological effects of root exudates containing allelochemicals on plants in field soil during continuous monoculture requires further evaluation. In this study, we hypothesized that root exudates represent a growth regulator in peanut–soil microorganism feedback processes, which leads to the progressive depletion of soil microorganisms during peanut monoculture. We further hypothesized that these microbial changes play a principal role in soil sickness rather than direct allelopathy.

Peanuts are increasingly grown on the same land without crop rotation due to limited amounts of arable land and intensive regional agro-industrialization. Such intensive peanut production is particularly widespread in the subtropical regions of China. However, its consecutive monoculture might have caused a continuous decline in yield and quality and increased susceptibility to diseases (Li et al., 2012). Therefore, the primary aims of this research were to study: 1) the predominant phenolic acids in peanut root exudates and their retention characteristics in an Udic Ferrosol; 2) whether the residual amount of these phenolic acids induced allelopathy on plant growth; 3) the effects of peanut root exudates on the abundance and composition of microbial communities. In addition, we also investigated the potential effects of the exudates on the specific group of rhizospheric bacteria (e.g., pseudomonads) using group-specific PCR primers. This microbial group was selected for study because they are common rhizobacteria that are known to interact with plant roots, acting as biological control agents, plant-growth promoters, and biodegraders of organic substrates including root exudates (Lorenzo, 2000; Dell'Amico et al., 2005).

2. Materials and methods

2.1. Peanuts and soil

Two peanut varieties generally planted on a large-scale in the subtropical regions of China were selected. Guanhua-5 (GH), which was derived from the parental peanut strain Yueyou551-11 by radiation, was cultivated by the reclamation farm of Liu-Jia station, Yingtan, Jiangxi Province, China and was the main planted variety in the hilly regions of Jiangxi Province, China. The Quanhua-7 (QH) strain, which was derived by the sexual hybridization of “028-9” (female parent) and “205-1” (male parent), was cultivated by the Quanzhou Institute of Agricultural Sciences and was the main planted variety in the hilly regions of the Fujian Province, China. Both varieties were universally subjected to consecutive monoculture in these regions, and experienced the soil sickness in the long-term monocropping fields.

Soil samples were collected from a fallow agricultural field at the Ecological Experimental Station of Red Soil, Chinese Academy of Sciences (China, 28°13'N and 116°55'E). The field selected was planted with peanut plants 5 years ago and was fallow thereafter. The soil was classified as Udic Ferrosol [FAO (1998) classification] and is generally referred to as red soil in China. Soil was taken from the surface layer (0–20 cm), sieved moist (2 mm), after removal of visible coarse plant material, and divided to two parts for air-drying to determine the physical and chemical properties of soil and for storage at 4 °C for all other experiments in this study. The nutrient composition of the soil was as follows: pH (H₂O) 5.1, organic matter 9.5 g kg⁻¹, total N 0.6 g kg⁻¹, total P 0.3 g kg⁻¹, total K 5.7 g kg⁻¹, available P 10.3 mg kg⁻¹ and available K 113.8 mg kg⁻¹.

2.2. Collection and treatment of peanut root exudates

Peanut seeds were surface-disinfected in 0.5% sodium hypochlorite (NaOCl) for 5 min, followed by three washes in sterile,

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