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Alleviation of take-all in wheat by the earthworm *Aporrectodea caliginosa* (Savigny)

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ABSTRACT

Take-all, caused by the fungus *Gaeumannomyces graminis* var. *tritici* (*Ggt*), can result in significant wheat (*Triticum aestivum*) yield losses. Previous research has suggested that earthworms may help to alleviate take-all severity, but the mechanisms are still not well understood. A pot experiment was conducted to investigate the effect of earthworms on take-all severity and crop responses for wheat grown in soils with contrasting levels of take-all suppression. The experiment consisted of eight treatment combinations composed of: two soils (suppressive and non-suppressive), with high or low quantities of added *Ggt* inoculum, and with or without additions of adult earthworms (*Aporrectodea caliginosa,* Savigny; the predominant species in New Zealand agricultural soils). Wheat plants were grown in the pots and destructively harvested at three growth stages over the full growing season. Large differences in take-all severity were observed, depending mainly on the degree of soil suppression and amount of inoculum added. Disease severity was greatest in non-suppressive (NS) soil with high inoculum (HI) and least in suppressive soil (S) with low inoculum (LI). When disease pressure was high (i.e. NS and/or HI), earthworms were associated with an average reduction in disease severity of 25% and average increases in plant production of 10%. Earthworms had only a small effect on decomposition of the *Ggt*-infected wheat residue used as inoculum. Therefore, it is likely that the disease mitigating effect of earthworms was not associated with a reduction in inoculum through enhanced wheat residue decomposition, but may be due to other factors such as increased dispersion and promotion of *Ggt* antagonistic microbes. However, additional research is needed to test this hypothesis and evaluate other possible mechanisms of earthworm mediated suppression of take-all. The results suggest that relatively small earthworm populations (200–300 m^{-2}) may be sufficient to provide a degree of control where disease pressure is high. A positive correlation between earthworm reproductive success and suppressive soil properties was also noted and this study appears to be the first to observe this. Further work is needed under field conditions to determine if management practices that help to sustain or enhance earthworm populations (e.g. reduced tillage) can contribute to improved cultural control of take-all.

1. Introduction

Earthworms are regarded as "ecosystem engineers" that improve physical, chemical and biological properties of soil. In cropping systems they facilitate plant residue decomposition, improve soil structure, and increase nutrient availability, among many other ecosystem services (Elmer, 2009; Francis and Fraser, 1998; Fraser et al., 2003; Lee, 1985; Mele and Carter, 1999; Scheu, 2003; Subler et al., 1997). More than 75% of studies have shown increased plant growth in the presence of earthworms (Blouin et al., 2006; Scheu, 2003). One of the hypotheses advanced to explain why earthworms promote plant production is that they decrease the incidence and severity of soil-borne plant diseases (Doran and Zeiss, 2000), such as take-all (Stephens et al., 1994), *Rhizoctonia* bare-patch (Stephens and Davoren, 1997), and *Fusarium* and *Verticillium* wilt (Elmer, 2009).

Take-all, caused by the soil-borne fungus *Gaeumannomyces graminis* (Sacc.) Von Arx & Olivier var. *tritici* Walker (*Ggt*), is a serious root disease of wheat (*Triticum aestivum*) worldwide (Cook, 2003; Duffy et al., 1997; Mathre et al., 1998). The economic cost of the disease can be significant, with potential yield losses reported to be greater than 40% (Conner et al., 2000). Residues from infected plants act as inoculum sources for the infection of the subsequent crop (Shipton, 1981). Take-all is difficult to control as there are no

Abbreviations: *Ggt*, *Gaeumannomyces graminis* var. *tritici*.

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disease-resistant wheat cultivars and chemical control of soil-borne diseases is not economical (Cook, 2003). However, take-all can be alleviated by crop rotation using non-susceptible hosts, or the development of take-all decline (TAD), which may occur after several successive years of wheat monoculture (Cook, 2003; Raaijmakers et al., 2009). TAD is a microbially mediated natural phenomenon where soil develops high rates of suppression - usually following a severe outbreak of disease (Weller et al., 2002).

Although suppression of take-all in wheat has been the subject of many studies, research into the potential role of earthworms in suppressing take-all is limited. Reported earthworm effects have ranged from no disease mitigation (Clapperton et al., 2001), to reduction of disease severity at only low rates of disease (i.e. no *Ggt* inoculum added) (Stephens and Davoren, 1996), and decreases in disease severity at high rates of disease (i.e. *Ggt* inoculum added) (Stephens et al., 1994). In all these studies, earthworms were reported to improve plant productivity. The mechanisms whereby earthworms affect disease severity are still not well understood. Limited consideration has been given to the possible link between the effect of earthworms enhancing decomposition of *Ggt*-infected residue and subsequent mitigation of disease severity.

The endogeic earthworm, *Aporrectodea caliginosa* (Savigny), is widely distributed throughout the world, and commonly constitutes over 80% of the earthworms found in New Zealand agricultural soils (Fraser et al., 1996). Although this species preferentially consumes the mineral component of topsoil and subsoil (Francis and Fraser, 1998; Lee, 1985), it may promote residue decomposition and therefore have a role in managing take-all in agricultural soils. While the effect of *A. caliginosa* on growth of wheat infected by *Ggt* has been investigated (Puga-Freitas, 2012), its role in reducing soil *Ggt* inoculum and the subsequent take-all severity, especially in soils exhibiting different degrees of suppression to the disease, has not been explored. The aims of the current study were to determine (1) whether earthworms influence take-all severity on wheat grown in either suppressive or non-suppressive soils, and (2) whether the earthworms' activities are effective in promoting the decomposition of *Ggt*-infected wheat residue (i.e. *Ggt* inoculum).

2. Materials and methods

2.1. Soil sampling and analyses

Two test soils, both Chertsey silt loam [Typic Dystrustept (USDA), Pallic Orthic Brown soil (New Zealand classification)] were collected (March 2011) from plots in Chertsey, New Zealand (43° 47′ 32.48″ S, 171° 57′ 38.41″ E), that had been under either second- or third-year wheat. A previous field study established that the plots had contrasting soil *Ggt* DNA inoculum concentrations and that the crops grown in them also had different take-all severity. Soil *Ggt* DNA concentrations were analysed by the South Australia Research and Development Institute (SARDI) following the methods described by Bithell et al. (2012), and take-all severity (i.e. crop take-all index, TAI, estimated on a scale of 0–100) using the method of Hornby et al. (1998). The second-year wheat soil had a high *Ggt* DNA concentration (223 pg g^{-1}) and the crop had high take-all severity (TAI = 32), while the third-year wheat soil had a low *Ggt* DNA concentration (50 pg g^{-1}) and almost no take-all in the crop (TAI = 1). In the present study, the second-year wheat soil was designated as the non-suppressive soil and the third-year wheat soil as the tentative suppressive soil. The suppressive properties of the two soils were confirmed in a preliminary experiment (data not presented) after the methods of Chng et al. (2013).

The top 15 cm layer was removed from an area of ~8 m^2 in each plot and transported to the laboratory, where the soil was sieved (<4 mm) to remove coarse material and earthworms (excluding any cocoons that passed through the sieve), and homogenised. The sieved soil was stored in field moist condition before use. A subsample was air-dried and used for determination of soil chemical and physical characteristics by standard procedures [soil pH using a glass electrode and a 1:2 soil/water ratio; total exchangeable acidity (H^+ and Al^{3+}) by extraction with 1 M KCl and determined by titration with 0.1 M NaOH (Sims, 1996); Olsen P by extraction with 0.5 M $NaHCO_3$ (pH 8.5) (Olsen et al., 1954); cation exchange capacity at pH 7 by the ammonium acetate method (Thomas, 1982); particle size distribution by sieving and sedimentation after soil dispersion by ultrasonic vibration (Gee and Or, 2002); particulate organic carbon (POM-C, macro-organic particles >50 μm diameter) (Gregorich and Beare, 2008), and total C and nitrogen (N) by the Dumas combustion method using a Leco TruSpec CN analyser (Leco Australia Pty. NSW, Australia) operating at 950 °C; Table 1].

2.2. Inoculum

The main source of inoculum used in this study was *Ggt*-infected wheat residue (straw and roots) collected from the non-suppressive field plot. The inoculum was washed free of soil, air-dried, separated into straw and roots, and cut into 5 cm-long pieces.

Ggt-infected roots of wheat seedlings (produced in a growth chamber) were used as additional fresh inoculum. Infection was achieved by placing plugs of potato dextrose agar (PDA) grown with *Ggt* in close proximity to the roots and maintained at 23 °C for 2 weeks before the experiment (Chng et al., 2005).

2.3. Pot experiment set-up and management

A pot experiment was conducted in shade houses in Lincoln, New Zealand (mean annual temperature 11.4 °C, mean annual rainfall 680 mm), from May 2011 (late autumn) to January 2012 (mid-summer) to mimic the normal growth cycle of autumn-sown wheat in New Zealand. Mean monthly temperatures and ranges during the experiment are given in Table 2. The experiment consisted of eight treatment combinations composed of: (1) two soils (suppressive, S; non-suppressive, NS), (2) with high (HI) or low (LI) amounts of added *Ggt* inoculum, and (3) with or without additions of adult earthworms (*A. caliginosa*). These combinations were replicated four times and then tripled to accommodate

Table 1
Physical and chemical properties of the take-all non-suppressive and suppressive soils used in the pot experiment.

Soil	pH	Exch. acidity[a] (cmol kg^{-1})	CEC[b] (cmol kg^{-1})	Base sat.[c] (%)	Olsen P (mg kg^{-1})	Total C (g kg^{-1})	Total N (g kg^{-1})	POM[d]-C (g kg^{-1})	Sand (g kg^{-1})	Clay (g kg^{-1})
Non-suppressive	6.3	0.22	13	61	22	25	2.5	2.9	133	175
Suppressive	5.8	0.27	13	61	26	25	2.5	2.6	151	150

[a] Exch. acidity: total exchangeable acidity.
[b] CEC: cation exchange capacity.
[c] Base sat.: base saturation = exchangeable bases (ΣCa + Mg + K + Na) as a percentage of CEC.
[d] POM: particulate organic matter.