REGULAR ARTICLE

Effects of take-all *(Gaeumannomyces graminis* var. *tritici)* on crop N uptake and residual mineral N in soil at harvest of winter wheat

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Abstract

Background and aims Take-all, caused by the fungus *Gaeumannomyces graminis var. tritici*, is the most damaging root disease of wheat. A severe attack often leads to premature ripening and death of the plant resulting in a reduction in grain yield and effects on grain quality (Gutteridge et al. in Pest Manag Sci 59:215–224, 2003). Premature death of the plant could also lead to inefficient use of applied nitrogen (Macdonald et al. in J Agric Sci 129(2):125–154, 1997). The aim of this study was to determine crop N uptake and the amount of residual mineral N in the soil after harvest where different severities of take-all had occurred.

Methods Plant and soil samples were taken at anthesis and final harvest from areas showing good and poor growth (later confirmed to be caused by take-all disease) in three winter wheat crops grown on the same soil type on Rothamsted Farm in SE England in 1995, 2007 and 2008 (harvest sampling only). All crops received fertiliser N in spring at recomended rates (190–200 kg N ha⁻¹). On each ocassion crops were assessed for severity of take-all infection (TAR) and crop N uptakes and soil nitrate plus ammonium (SMN) was determined. Grain yields were also measured.

Results Grain yields (at 85% dry matter) of crops with moderate infection (good crops) ranged from 4.3 to

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A. J. Macdonald (⊠) · R. J. Gutteridge Rothamsted Research, Harpenden, Herts, UK AL5 2JQ e-mail: andy.macdonald@rothamsted.ac.uk 13.0 t ha^{-1} , compared with only 0.9–4.5 t ha⁻¹ for those with severe infection (poor crops). There were significant (P < 0.05) negative relationships between crop N uptake and TAR at anthesis and final harvest. At harvest, good crops contained 129-245 kg N ha⁻¹ in grain, straw and stubble, of which 85-200 kg N ha⁻¹ was in the grain. In contrast, poor crops contained only 46–121 kg N ha⁻¹, of which only 22–87 kg N ha⁻¹ was in the grain. Positive relationships between SMN and TAR were found at anthesis and final harvest. The SMN in the 0-50 cm layer following harvest of poor crops was significantly (P < 0.05) greater than that under good crops, and most (73-93%) was present as nitrate. Conclusions Localised patches of severe take-all infection decreased the efficiency with which hexaploid wheat plants recovered soil and fertiliser derived N, and increased the subsequent risk of nitrate leaching. The risk of gaseous N losses to the atmosphere from these areas may also have been enhanced.

Keywords Winter wheat \cdot Take-all fungus \cdot Nitrogen \cdot Nitrate \cdot Ammonium \cdot Leaching \cdot Denitrification

Abbreviations

TAR	Take-all rating	
SMN	Soil mineral N	

GS Growth Stage (Zadocks et al. 1974)

Introduction

Increasing concern about greenhouse gas emissions (both CO_2 and N_2O), produced during the manufac-

ture and use of N fertilisers (Smith et al. 1997) and nitrate losses from agricultural land within Nitrate Vulnerable Zones in Europe (Anon 2000; Anon 2008; www.defra.gov.uk/environment/water/quality/nitrate/), together with the need to increase global food production to feed a growing world population, has highlighted an urgent need to maximise the efficiency of N fertiliser use on both environmental and economic grounds (Dourado-Neto et al. 2010). However, to achieve this requires an improved understanding of the factors which control the uptake and assimilation of N by arable crops. Cereals represent a substantial proportion of the arable acreage in England and elsewhere in Europe. Consequently, improved efficiency of N use by winter wheat (Triticum aestivum) is an important goal for agronomists and plant scientists. Macdonald et al. (1997) reported that the efficiency of fertiliser N uptake by winter wheat was substantially decreased when the crop was severely infected with the Ascomycete Gaeumannomyces graminis var. tritici (Walker 1981) which infects the roots and causes take-all disease. Also, more residual inorganic N (ammonium and nitrate) was present in the soil following harvest compared with a healthy crop. The take-all fungus is soil-borne and is particularly prevalent in second wheat crops. Severely infected plants are often stunted and ripen prematurely, causing whiteheads (Gutteridge et al. 2003). The disease attacks the root system and diminishes the plant capacity to take up nutrients, including nitrogen (Hornby et al. 1998). However, relatively little detailed information exists in the literature on the effects of take-all on crop N uptake and residual mineral N in soil. Consequently, a series of three field studies were done to examine the nature of the relationship between take-all infection and residual mineral N in the soil at harvest of winter wheat, with a view to evaluating the likely impact of take-all infection on the efficiency of crop N uptake and the risk of subsequent N losses.

Materials and methods

Crop and soil sampling

In early May 1995 patches of uneven growth (later confirmed to be caused by take-all) were seen in a winter wheat crop grown on a flinty silty clay loam at Rothamsted (Table 1). The soil was classified as Batcombe series (Table 1). The top-soil layer (0-23 cm) contained about 28% clay, 51% silt, 14% fine sand and 6% coarse sand. Further details of soil properties are given in Powlson et al. (1986). Around anthesis (GS 59) whole crop samples were taken from six separate areas (three of which showed stunted growth), each measuring 0.5×0.5 m. Plants were washed free of soil and their root systems examined for take-all. The proportion of each root system infected was graded as slight (<25% of roots infected), moderate (25-75%) or severe (>75%). From these gradings a weighted take-all rating (TAR) was calculated: TAR = 1(% of plants with)slight infection) + 2 (% of moderate infection) + 3 (% severe infection); thus Maximum TAR = 300(Dyke and Slope 1978). The plants were then weighed, chopped, dried and ground. Crop samples were taken at harvest from six additional areas within the same field (Table 1.), three of which showed signs of take-all. The plants were assessed individually for take-all as described above. Crops were threshed to obtain separate samples of grain, straw and chaff, and stubble. These were weighed, dried and ground prior to determination of their total N content.

In June (GS 59), soil samples were taken by hand to a depth of 20 cm from each of the six initial sampling areas, soon after the plants were removed, using a gouge auger of 2.5 cm diameter (Table 1). The soil samples were stored frozen prior to analyses for mineral N (nitrate plus ammonium). Soil samples (0-25 and 25-50 cm) were taken from each of the six additional areas following harvest, using a hydraulic soil sampler (Hydro Care MCL 2). After thawing, soil samples were sieved <6.4 mm and 62.5 g of fresh soil was extracted with 200 ml of 2 M KCl by shaking for one hour. Filtered soil extracts were analysed colorimetrically using an ALPKEM auto-analyser, to determine their nitrate and ammonium contents (Henriksen and Selmer-Olsen 1970; Krom 1980). Soil mineral N (SMN) contents (kg N ha⁻¹) were calculated using soil weights from a previous experiment located on the same soil type (Powlson et al. 1986). Sub-samples of dried, ground plant material were analysed for total N by combustion, using a LECO 2000 CNS elemental analyser (LECO Instrument Ltd, Stockport, UK).

Table 1 Details of field sites and crops, and plant and soil sampling (1995-2008)

Field Site ^a	Wheat variety	Sowing date	Fertiliser N application		Harvest date	Crop sampling		Soil sampling	
			Date	Rate (kg N ha ⁻¹)		Date	GS	Date	Depths (cm)
Little Knott	Mercia	12/09/1994	13/03/1995	40 ^b	02/08/1995	01/06/95	59	01/06/95	0-20
			13/04/1995	160 ^b	-	31/07/95	91	02/08/95	0-25,25-50
New Zealand	Brompton	27/09/2006	15/03/2007	40 ^c	09/08/2007	07/06/07	69	07/06/07	0-20
			26/04/2007	150 ^b	-	25/07/07	91	27/07/07	0-25,25-50
Stackyard	Brompton	07/10/2007	28/02/2008	36 ^c	19/09/2008	08/08/08	91	08/08/08	0-25,25-50
			24/04/2008	160 ^c	-	_	-	_	_

^a All three field sites were located on a flinty, silty clay loam (Batcombe or Heavy Batcombe series); USDA: Aquic (or Typic) Paleudalf, FAO: Chromic (or Vertic) Luvisol (Avery and Catt 1995).

^b N applied as Nitraprill (34.5% N); ^c N applied as Double Top (27.0% N)

Similar programmes of crop and soil sampling were undertaken in 2007 and 2008 on two additional field sites, with similar soil properties, at Rothamsted (Table 1), but in these studies eight areas were sampled within each crop, four of which showed symptoms of take-all, and soil samples were taken by hand using a gouge auger. In both years take-all assessments and determinations of crop N uptake and SMN were done as described above. In 2008 crop and soil samples were taken at harvest only. All three field sites were in long-term arable cropping (mostly cereals) for several years before the studies began, and had received sufficient lime, P and K inputs to ensure growth was not limited by P, K or pH. All three of the crops studied received split N fertiliser applications in spring, consistent with recommended rates (Table 1).

Statistical analyses

Plant and soil data were analysed statistically using Genstat[®] (2010). Unpaired T-tests were done to examine differences in crop N uptake and residual soil mineral N (0–20 cm) between plants with moderate or severe take-all ratings (TAR) at anthesis. In the subsequent text we refer to crops with small and large TAR as "Good" and "Poor" crops, respectively. Harvest data, including grain yield at 85% dry matter, crop N uptake and residual SMN (0–25, 25–50 and 0–50 cm), were analysed by one way analysis of variance comparing plants with moderate and severe take-all ratings, with years as blocks. Significance, where stated, was at the 5% level or less. The relationships between whole crop N uptakes and TAR, and SMN and TAR, were examined using the trend line facility in Excel® (2007) and the simple linear regression facility in Genstat®. Four residual degrees of freedom were used to test levels of significance (F pr) for the linear regressions in 1995 (Fig. 1a & b), but in 2007 and 2008 (Fig. 1c, d, e & f) residuals had six degrees of freedom. In all cases regressions had only one degree of freedom. In 2007 some values used in the regression analyses (Fig. 1c & d) had high leverage, and in 2008 one regression (Fig. 1f) contained large standardised residuals.

Results

Effects of take-all at anthesis

At anthesis 1995 and 2007, take-all ratings (TAR) for the good crops averaged 165 and 224, respectively. Corresponding ratings for poor crops averaged 292 and 299. Consequently, only in 1995 was the good crop TAR significantly smaller than the poor crop. Despite this, good crop N uptakes averaged 205 and 167 kg N ha⁻¹ in 1995 and 2007 respectively, and were significantly greater than the corresponding uptakes for poor crops, which averaged only 71 and 31 kg N ha⁻¹ respectively. In both years there was a strong negative relationship (P<0.05) between crop N uptake and TAR (Fig. 1a and c) at anthesis. In 1995 the SMN present in the

b)

y = 0.6063x + 38.303

 $R^2 = 0.8794$

200

d)

= 0.3357x - 10.312

200

f)

y = 0.4166x - 20.77 $R^2 = 0.5993$

200

TAR

 $R^2 = 0.2655$

TAR

y = 0.5024x + 8.3742

 $R^2 = 0.4872$

300

y = 3.2344x - 857.42

 $R^2 = 0.7388$

300

300

300

250

200

150

100

50

0

300

250

200

150

100

50

0

300

250

200

150

100

50

0

100

SMN, kg N ha⁻¹

100

SMN, kg N ha⁻¹

100

SMN, kg N ha⁻¹



Fig. 1 The relationship between a) Take-all infection (TAR) and whole crop N uptake by winter wheat at anthesis (\Box) and harvest (\bullet) and b) between TAR and SMN at anthesis (0-

top-soil (0–20 cm) ranged from 100 to 223 kg N ha^{-1} and was substantially greater than the 41– 149 kg N ha^{-1} found in 2007. This was almost certainly due to greater nitrate leaching soon after fertiliser application in 2007, when rainfall in May totalled 136 mm prior to sampling, compared with only 28 mm in 1995. In 1995 and 2007 SMN in topsoil (0–20 cm) under good crops averaged 140 and 62 kg N ha^{-1} respectively. In both cases the



TAR

corresponding amounts under poor crops were greater, averaging 213 and 93 kg N ha⁻¹ respectively, but only in 1995 was the difference significant. In contrast to the negative relationship between crop N uptake and TAR, a strong positive relationship (P<0.05) was found between the quantity of SMN present in the soil (0–20 cm) and TAR in 1995 (Fig. 1b), but this relationship was weaker (P>0.1) in 2007 (Fig. 1d).

Effects of take-all at final harvest

In all 3 years poor crops had very severe take-all, with TARs averaging 289, 300 and 285 in 1995, 2007 and 2008 respectively. Corresponding TARs for good crops were 178, 291 and 154. Consequently, take-all infection in poor crops at harvest 1995 and 2008 was significantly greater than in good crops, but was not significantly different in 2007. In all 3 years there was a negative relationship (P < 0.05) between take-all severity and crop N uptake at harvest (Fig. 1 a, c & e), with severely infected crops containing less N than those with moderate infection, as was found at anthesis in 1995 and 2007. In all cases the grain yield and N uptake of good crops was significantly greater than that of poor crops, and residual SMN was significantly smaller (Fig. 2 a, b & c). In all 3 years there was a positive relationship between residual SMN (0-50 cm) and TAR, but it was only significant (P < 0.05) in 2007 and 2008.

In 1995, grain yields of wheat with severe takeall infection (poor crop) averaged 0.9 t ha^{-1} , compared with 4.3 t ha⁻¹ for wheat with moderate infection (good crop). In 2007 and 2008 yields for good crops were 6.7 and 13.0 t ha⁻¹, respectively. Corresponding yields for poor crops were only 1.1 and 4.5 t ha⁻¹. Good wheat crops contained on average 129-245 kg N ha⁻¹ in grain, straw and stubble, of which 85–200 kg N ha⁻¹ was in the grain (Fig. 2a). In contrast, poor crops contained on average only 46-121 kg N ha⁻¹, of which 22-87 kg N ha⁻¹ was in the grain. Mean grain N concentrations for poor crops ranged from 2.29 to 2.84%N over all 3 years (1995, 2005 & 2007) and were similar or greater than those for good crops, which ranged from 1.81 to 2.31%N. In all cases SMN in the 0-50 cm layer following harvest of poor crops was significantly greater than that under good crops; averaging 98-150 kg N ha⁻¹ compared with 44-102 kg N ha⁻¹ (Fig. 2). Most (73-93%) of the SMN remaining under both good and poor crops (0-50 cm) was present as nitrate, and most of this was present in the top-soil layer (0-25 cm); except at harvest 2007 when substantial amounts were found in the sub-soil (25-50 cm; Fig. 2b). This was almost certainly due to nitrate leaching following the heavy rainfall in May.





Fig. 2 Crop N uptake and residual SMN (0-25 & 25-50 cm) under Good and Poor crops at harvest (a) 1995, (b) 2007 and (c) 2008, with \pm SE on whole crop N plus SMN (0–50 cm)

Discussion

а

kg N ha-1 200

b

kg N ha-1 200

350 300

250

150

100

50

0

350

300

250

150

100

50

Ô

Effects of take all on crop N uptake and residual mineral N in soil

In all 3 years the N accounted for in the whole crop plus SMN (0-50 cm) under good crops was greater than that for poor crops (Fig. 2 a, b & c). The differences between good and poor crops averaged 27, 105 and 70 kg N ha⁻¹ in 1995, 2007 and 2008 respectively. The largest difference was apparent in 2007 when rainfall following fertiliser applications (April-July) totalled 298 mm; substantially more than that in 1995 and 2008 when rainfall totalled 86 and 266 mm respectively. The large amount of SMN present in sub-soil (25-50 cm) under the poor crop in 2007 (Fig. 2b) indicates that some of the N unaccounted for in crop plus SMN was leached below 50 cm, and some may have been lost to the atmosphere, by denitrification (Addiscott and Powlson 1992; Macdonald et al. 1997; Powlson et al. 1986; Recous et al. 1988; Smith et al. 1997). The soil type at all three sites was very similar (Table 1). Consequently, differences in crop N uptake and residual SMN were most likely to be due to growing season effects (differences in temperature, rainfall etc.) rather than soil effects.

The similar (or greater) grain N concentration observed in the lower yielding "poor" crops compared with "good" crops indicates that the smaller N uptake of the former was not primarily due to lack of available N. Therefore, it was most almost certainly due to a decrease in the capacity of the crop to access this N. Smith et al. (2004) acknowledged that take-all infection decreases access to soil mineral N by the wheat crop because of the damage caused to its root system. The root damage caused by severe take-all infection in the work reported here almost certainly decreased uptake of both water and nutrients, resulting in decreased crop growth and yield potential. Therefore, the smaller N uptake of the "poor" crop reported in this study is a consequence of severe take-all infection, rather than its primary effect.

Whilst the impact of severe take-all on the efficiency of nitrogen fertiliser recovery by winter wheat cannot be determined directly from these data it is possible to estimate its impact assuming that part of the decrease in crop N uptake due to severe take-all (75–145 kg N ha⁻¹) was due to poorer recovery of fertiliser N. Macdonald et al. (1997) reported that, at harvest, winter wheat crops grown on a similar soil type at Rothamsted in 1986 and 1987 recovered 56% of the ¹⁵N-labelled fertiliser applied. However, fertiliser N accounted for about 62% of the total crop N uptake. Assuming that 62% of the decrease in crop N uptake due to severe take-all (i.e. the difference between N uptake of a good and poor crop) was due

to decreased recovery of fertiliser N, we estimated that severe take-all decreased fertiliser N uptake by $47-90 \text{ kg ha}^{-1}$; or 23–47% (average of 37%) of that applied. However, the efficiency of fertiliser uptake by plants severely infected with take-all may well be less than for a healthy crop, so decreases in fertiliser N uptake may well be greater than this estimate. Consequently, severe take-all decreased the capacity of the crop to recover both soil and fertiliser-derived N, and increased the risk of N losses during the growing season and the post-harvest period.

However, at harvest 2007, good crops contained substantial amounts of N despite having severe take all infection (Fig. 2b). A one tailed t-test (unpaired) indicated that a significant increase in the mean TAR for good crops, from 224 to 291, occurred between anthesis and harvest (Fig. 1c). Therefore, plants in patches of good growth may have recovered much of their N requirement by anthesis, prior to the onset of severe infection. The wet conditions prior to anthesis may well have offset the effects of take-all to some extent and helped maintain crop N uptake. This is consistent with work reported by Recous et al. (1988) which indicated that uptake of ¹⁵N-labelled fertiliser reached a maximum at flowering. Therefore, the growth stage at which severe takeall infection develops may be critical to the efficiency with which cereals recover both fertiliser and soil derived N, and weather conditions or management practices which delay the onset of infection, or counteract its effects prior to anthesis, may help maintain crop N uptake and minimise N losses to the environment. Relationships between SMN and take all infection at anthesis and harvest were in all cases positive (Fig. 1 b, d & f), indicating that severe infection restricted crop N uptake and resulted in substantially more mineral N (mostly nitrate) remaining in the soil at harvest compared with that left under plants with only moderate infection.

Management practices to mitigate the effects of take-all

It is apparent from this work that wheat crops at risk of take-all infection present an enhanced risk of N losses to the environment. Modifications to crop management practices may help to minimise the risk of developing severe take-all. In particular, increasing the frequency of break crops in arable rotations may be helpful (Dyke and Slope 1978). However, where severe infection occurs, the early establishment of a break crop or cover crop (Macdonald et al. 2005) may help utilize the large amounts of SMN present in soil; alternatively, subsequent winter sown crops may require less fertilizer N. The use of spatial information in decision support systems (Falloon et al. 1999; Smith et al. 1996) to account for the distribution of severe take-all infection within fields may help target N fertiliser applications to take account of its impact on the amount and distribution of residual mineral N available to subsequent crops. A similar approach may help adjust fertilizer application rates to account for other factors which also limit crop N uptake (e.g. pests, drought and other diseases) and enhance SMN available for subsequent crop uptake or losses to the environment.

The risk of a susceptible crop to take-all is largely dependent on the amount of infective inoculum present at the time of sowing. Agronomic and husbandry practices can influence the risk of take-all; for example, factors which encourage the disease are soils deficient in either phosphate or potash (below index 2), presence of efficient carriers of the take-all fungus (rhizomatous grasses, cereal volunteers), and early sowing date. Despite attention to reduce the impact of these factors which encourage take-all, severe disease can still occur. Recent evidence suggests that winter wheat cultivars, when grown as a first crop, can differ in their ability to build-up the take-all fungus in the soil (McMillan et al. 2011). This finding provides a new approach to reduce the take-all inoculum in the soil, thereby, reducing the take-all risk to a second wheat crop.

Conclusions

In summary, severe take-all infection of winter wheat significantly decreased the crop's capacity to take up nitrogen, whether from fertiliser N or the soil reserves. This substantially increased the amount of SMN (mostly nitrate) present in soil at harvest at risk to subsequent losses. Severe take-all infection decreased the recovery of fertiliser N by about 37% of that applied. Consequently, take-all increased the risk of nitrate leaching from severely infected patches of arable land in the autumn and winter following harvest, and may also have enhanced the risk of gaseous N losses (including N_2O) to the atmosphere during the growing season (Smith et al. 1997). Management practices which delay the onset of severe take-all infection until after anthesis may help maintain crop N uptake and minimise the risk of N losses. Larger scale studies are required to examine the wider effects of take-all infection on fertiliser N uptake and losses to the environment.

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