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Evidence that wheat cultivars differ in their ability to build up inoculum of the take-all fungus, *Gaeumannomyces graminis* var. *tritici*, under a first wheat crop

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The effect of wheat cultivar on the build-up of take-all inoculum during a first wheat crop was measured after harvest using a soil core bioassay in field experiments over five growing seasons (2003–2008). Cultivar differences in individual years were explored by analysis of variance and a cross-season Residual Maximum Likelihood (REML) variance components analysis was used to compare differences in those cultivars present in all years. Differences between cultivars in the build-up of inoculum were close to or at significance in two of the five trial years (2004 $P < 0{\cdot}05$; 2006 $P < 0{\cdot}07$), and current commercially listed cultivars were represented at both extremes of the range. In 2007 and 2008, when environmental conditions were most favourable for inoculum build-up, differences were not significant ($P < 0{\cdot}3$). In 2005 the presence of *Phialophora* spp. at the trial site restricted the build-up of take-all inoculum under all cultivars. The cross season REML variance components analysis detected significant differences (range: 3·4–47·8% roots infected in the soil core bioassay; $P < 0{\cdot}01$) between the nine cultivars present in all years (excluding 2005). This is the first evidence of relatively consistent differences between hexaploid wheat cultivars in their interactions with the take-all fungus, and this could give an indication of those cultivars that could be grown as a first wheat crop, in order to reduce the risk of damaging take-all in a second wheat crop. This phenomenon has been named the take-all inoculum build-up (TAB) trait.

Keywords: hexaploid wheat genotypes, inoculum build-up, *Phialophora* spp., soil core bioassay, take-all disease, *Triticum aestivum*

Introduction

Take-all, caused by the soil-borne ascomycete fungus *Gaeumannomyces graminis* var. *tritici* (Ggt) (Walker, 1981), is a devastating root disease of wheat and a serious constraint on wheat productivity in the UK and worldwide (Hornby *et al.*, 1998). Typical take-all symptoms show as black necrotic lesions on the roots and, when severe, can spread to the stem base causing blackening (Skou, 1981). Hyphae spread through the roots and destroy the vascular tissue. If severe disease occurs, typical above ground symptoms can develop and show as stunted plants and whiteheads caused by the premature ripening of the crop. This significantly reduces grain yield and quality, and losses of up to 60% have been reported in the UK.

If consecutive wheat crops are grown, take-all is usually negligible in first wheats, most severe in years 2–4, and then decreases. The latter phenomenon is known as take-all decline (TAD) (Slope & Cox, 1964). TAD has been widely reported in the UK and Europe, but in Australia the dry and hot environment is reported to restrict the development of TAD (Yarham, 1981). Although first wheat crops usually show very little evidence of disease, they can build up inoculum in the soil rapidly from small founder populations so that severe disease can occur in a following wheat crop. In the UK and elsewhere in Europe, a large proportion of second and subsequent wheat crops are at risk from significant damage where take-all inoculum has developed.

After harvest of a susceptible crop, the take-all fungus survives saprotrophically on the dead roots and stem bases, and this forms the main source of inoculum for the next susceptible crop (Cook, 2003). However, Ggt is a relatively poor saprotrophic competitor so that survival of inoculum rapidly declines in the absence of a living host such as cereal volunteers and other efficient carriers of the take-all fungus (Shipton, 1981). Consequently, a 1 year break from susceptible cereals is usually sufficient to reduce inoculum levels to negligible amounts. Therefore, damaging take-all can largely be avoided by only growing one susceptible crop at a time in the crop rotation (Yarham, 1981). However, on most soils, and due to current economic conditions, there has been a trend to

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increase the proportion of susceptible hosts in wheat-based rotations as the intensity of cropping increases and non-cereal break crops become less profitable (Hornby *et al.*, 1998; Cook, 2003). Attempts to control take-all using chemical, biological and cultural methods have met with only limited success, and with wheat as the dominant UK crop for the cereal industry, take-all remains one of the most difficult and important diseases to control.

Predicting the risk of severe take-all has always been difficult as many agronomic and cultural practices, as well as climatic conditions, can have an impact on how the disease develops. A soil core bioassay, which measures the take-all infectivity of the soil, can give an indication of the potential risk to a following crop (Hornby, 1981). Such bioassays are very labour intensive and not, therefore, a practical option for assessing risk to commercial crops. However, the bioassay can be useful to study the biology of the disease in experimental situations and the percentage of roots infected in the bioassay after a first wheat crop is well correlated with observed amounts of take-all in both the spring and summer in the following second wheat crop (Hornby *et al.*, 1998; Gutteridge *et al.*, 2008).

The take-all infectivity of the soil, measured using the soil core bioassay, is widely interpreted as a gauge of the level of take-all inoculum in the soil (Hornby, 1981). However, the infectivity of the soil could also be influenced by the biological and chemical properties of the soil, which could suppress this disease (Hornby, 1983) or by the differing pathogenicity of Ggt isolates present in a particular field (Lebreton *et al.*, 2007). Recently, a molecular method (not currently available in the UK) has been developed in Australia to measure the amount of take-all DNA in soil samples from the field (Ophel-Keller *et al.*, 2008). This method directly quantifies the amount of take-all inoculum in the soil independently of other factors which may influence infectivity. Both Gutteridge *et al.* (2008) and Bithell *et al.* (2009) have since shown a good relationship between the DNA test and the soil core bioassay, thus supporting the interpretation that take-all inoculum levels are detected using the bioassay method.

Research done in the early 1980s, using the soil core bioassay method, suggested that two hexaploid wheat cultivars (Norman and Avalon), when grown as a first wheat, differed in their ability to build up take-all inoculum in the soil (Widdowson *et al.*, 1985). In recent years, first wheat field trials at Rothamsted, within the Wheat Genetic Improvement Network (WGIN; http://www.wgin.org.uk), have been used to study a wider range of cultivars and their differences in nitrogen use uptake and utilization efficiencies (Barraclough *et al.* (2010). It is the take-all inoculum data from these experiments that are reported in this paper.

Materials and methods

Field trial design

Field trials, one in each of the harvest years from 2004 to 2008, were all sited on the Rothamsted farm, Hertfordshire, UK, on flinty clay loam soil of the Batcombe soil series. The experiments were set up as fully randomized block designs; treatments included three replicates of a range of 20–32 wheat cultivars in factorial combination with 2, 3 or 4 different nitrogen rates (Table 1) (except the first year where cultivars were randomized in three blocks and N rates were arranged in four sub-blocks in each main block (Barraclough *et al.*, 2010)). Host genotypes included current commercial and semi-modern cultivars in the UK together with a smaller number of European origin.

All of the trials were grown as first wheat crops (sown after oats) and established in the autumn (including spring cultivars), as part of the WGIN programme investigating nitrogen use efficiency in European wheat cultivars (Barraclough *et al.*, 2010). Seed rates were mostly in the range 300–350 seeds m^{-1} but were sometimes larger due to poor performance in seed germination tests and late sowing of some plots (due to seed delivery). Growth regulator, herbicides and fungicides were applied according to the standard practice of the Rothamsted Farm.

Take-all inoculum build-up

A soil core bioassay (Slope *et al.*, 1979; Gutteridge *et al.*, 2008) was used to measure the infectivity of the soil after

Table 1 Details of field experiments[a] used to measure the take-all inoculum building ability of wheat cultivars over five field seasons from 2004 to 2008

Harvest year (Rothamsted field trial code)	Rothamsted field	Previous cropping history: Preceding year	Previous cropping history: 2 years previous	Sowing date	Plot size (m)	Treatments (cultivars × nitrogen rates)
2004 (04/R/WW/415)	Blackhorse	Springs oats	Winter oilseed rape	11–19/11/03[b]	10 × 3	32 × 4
2005 (05/R/WW/506)	Fosters	Winter oats	Winter wheat	11–13/10/04	16 × 3	20 × 2
2006 (06/R/WW/612)	Meadow	Winter oats	Spring oilseed rape	02–15/10/05	16 × 3	24 × 3
2007 (07/R/WW/702)	Blackhorse	Winter oats	Winter wheat	13–14/10/06	18 × 3	24 × 4
2008 (08/R/WW/816)	Meadow	Winter oats	Winter wheat	12–23/10/07	15 × 3	24 × 4

[a]Field experiments were done as part of the Wheat Genetic Improvement Network programme (http://www.wgin.org.uk) to study nitrogen use efficiency in wheat. Additional details on these field trials are given in Barraclough *et al.* (2010).
[b]Except cv. Chablis sown on 02/03/2004; cv. Paragon sown on 12/02/2004; cv. Zyta sown on 05/12/2003.

Table 2 Sampling information for the yearly first wheat field experiments from 2004 to 2008, in which wheat cultivars were assessed after harvest for their take-all inoculum building ability using a soil core bioassay

Harvest year	Date harvested	Number of cultivars sampled/total that year	Date sampled[a] (soil core bioassay)
2004	31/08/2004	10/32	03/09/2004
2005	11/08/2005	11/20	15/08/2005
2006	08/08/2006	16/24	23/08/2006
2007	30/08/2007	24/24	10/09/2007
2008	19/09/2008	24/24	02/10/2008

[a]Sampling was as soon after harvest as possible, weather permitting.

harvest from selected cultivars in years 2004–2006 and all cultivars in 2007 and 2008, at one nitrogen application rate (Table 2). The 200 kg N ha^{-1} was chosen for sampling because this is closest to commercial application rates. Five soil cores (5·5 cm diameter by 10 cm deep) were taken in a zig-zag transect across each plot. Cores were inverted into plastic drinking cups (11 cm tall with four drainage holes drilled in the bottom) which contained a basal layer of 50 cm^3 damp sand. The top of the inverted soil core was pressed to the sides of the cup. The soil was lightly watered and 10 wheat seeds (cv. Hereward (RAGT, Cambridge, UK)) placed on the surface (originally the bottom of the core). Seeds were covered with a layer of horticultural grit, and pots transferred to a controlled environment room for 5 weeks (16 h day, 70% RH, day/night temperatures 15/10°C and watered twice weekly). After 5 weeks the plants were removed and the roots washed out with water. The roots were assessed for take-all lesions in a white dish under water and the total numbers of plants and roots, and the numbers of plants and roots infected were recorded. The percentages of plants and roots infected were calculated as a measure of the infectivity of the soil.

Microscopic analysis

Roots with typical black take-all lesions viewed by eye in a white dish under water were recorded as above. In 2005 a large proportion of roots from the bioassay showed pale brown or grey discoloration and there was a noticeable lack of typical black take-all lesions. These discoloured roots were viewed under a binocular microscope (×25 objective, ×10 eyepiece) and swollen cells typical of *Phialophora graminicola* (anamorph of *G. cylindrosporus*) were seen on the grey roots, and *Phialophora* sp. lobed hyphopodia (probable anamorph of *G. graminis* var. *graminis*) on the pale brown roots (Hornby *et al.*, 1998).

Statistical analysis

The percentage of roots infected were transformed to logits and compared by analysis of variance using GENSTAT (VSNI). Significant effects were supposed when $P \leq 0{\cdot}05$. A cross-season Residual Maximum Likelihood (REML) variance components analysis was conducted for the nine cultivars that were tested in four of the five trial years (excluding 2005). In 2005, the high incidence of *Phialophora* spp. (as confirmed by microscopic analysis) restricted take-all inoculum build-up. Therefore these results were excluded from further analysis.

Results

The infectivity of the soil, measured using the soil core bioassay, revealed that the amount of take-all inoculum left after a first wheat crop varied depending on wheat cultivar grown (Table 3). In each experiment there was considerable variation in the amount of inoculum detected between replicate plots of the same wheat cultivar. This reflects the known inherent 'patchiness' of take-all in the field and the difficulties of conducting field trials to study the take-all fungus (Hornby, 1981). As a consequence, only two out of 5 years of the WGIN field trials sampled show significant differences or close to significant differences between cultivars in their ability to build up small populations of the take-all fungus during a first wheat crop (2004, $P < 0{\cdot}05$; 2006, $P < 0{\cdot}07$; Table 3). Results from 2007 and 2008, when overall amounts of inoculum were highest, were not significant ($P < 0{\cdot}3$). In 2005, inoculum levels were particularly low for all cultivars and any effect of cultivar on inoculum build-up was highly non-significant ($P < 0{\cdot}7$). In this bioassay year, the presence of two competing and weakly parasitic root colonizing fungi, *Phialophora graminicola* and *Phialophora* sp. lobed hyphopodia was detected by microscopy in moderate to high abundance in all samples.

The overall level of take-all inoculum, measured using the soil core bioassay, differed considerably between years (Table 3). This is most probably the result of annual differences in environmental conditions. The main period of inoculum build-up in a first wheat is from about May through to harvest (Slope & Gutteridge, 1979). In general, high temperatures and low rainfall limit inoculum build-up; conversely more moderate temperatures and higher rainfall, creating warm and moist soils, are more favourable (Hornby *et al.*, 1998). Conditions in 2007 (total rainfall in May to August, 359 mm; mean max temperatures in each of the 4 months 20°C or less; Table 4) were close to ideal, and this probably explains why amounts of inoculum were larger in that year than any other. However, in the other 4 years higher temperatures and/or lower rainfall during at least some part of this critical period probably explain, to a large extent, the generally smaller amounts of inoculum that were detected. In 2005, and as already indicated above, the presence of *Phialophora* spp. almost certainly inhibited the take-all fungus and contributed to the very limited development of inoculum in that year.

When a subset of wheat cultivars, which were sampled in all years, were analysed using a cross season REML variance components analysis, the results showed that

Table 3 Incidence of infected roots in the soil core bioassay used to measure the take-all inoculum building ability of winter wheat cultivars grown as first wheat crops and measured after harvest in field experiments from 2004 to 2008

	Logit % roots with take-all (back-transformed means)				
	Year				
Cultivar	2004	2005[a]	2006	2007	2008
Avalon	−1·92 (1·6)[b]	−1·68 (2·8)	−1·36 (5·6)	1·16 (90·6)	−1·24 (22·2)
Batis				0·25 (61·6)	−0·58 (35·8)
Beaver				1·11 (89·7)	−2·60 (6·5)
Cadenza	−2·29 (0·5)	−2·19 (0·7)	−1·91 (1·7)	−0·16 (41·7)	−3·97 (1·4)
Claire		−2·29 (0·5)	0·11 (54·8)	0·47 (71·3)	−3·30 (3·1)
Cordiale			−0·82 (15·7)	0·44 (70·1)	−3·12 (3·8)
Hereward	−0·19 (40·4)	−1·63 (3·2)	−0·65 (21·0)	1·42 (94·0)	−0·40 (40·2)
Hurley				0·66 (78·4)	−3·69 (2·0)
Istabraq		−1·39 (5·4)	−2·35 (0·4)	0·41 (69·1)	−0·61 (35·0)
Lynx			−1·59 (3·5)	0·17 (58·0)	−1·11 (24·6)
Malacca	−1·30 (6·5)	−2·26 (0·6)	−0·36 (32·1)	0·54 (74·0)	−0·78 (31·3)
Maris Widgeon				0·90 (85·4)	−3·36 (2·9)
Mercia	−1·71 (2·7)		−0·86 (14·6)	0·16 (57·4)	−1·09 (24·9)
Monopol	−0·73 (18·4)	−2·28 (0·5)	−0·97 (12·1)	0·34 (65·8)	−1·38 (19·7)
Napier			−1·84 (2·0)	0·63 (77·3)	−2·11 (10·4)
Paragon				0·93 (86·0)	−1·30 (21·2)
Rialto	−1·85 (1·9)				
Riband	−1·85 (1·9)	−2·92 (0·0)	−0·94 (12·7)	0·29 (63·7)	−1·97 (11·9)
Robigus		−2·47 (0·2)	−0·89 (13·8)	0·06 (52·4)	−2·17 (9·9)
Savannah				0·49 (72·1)	−1·93 (12·4)
Shamrock				0·54 (74·1)	0·21 (55·3)
Soissons	−0·43 (29·3)	−2·99 (0·0)	−2·08 (1·0)	0·39 (68·1)	0·23 (55·8)
Sokrates				0·33 (65·5)	−2·71 (5·8)
Solstice			−0·85 (14·9)	0·17 (58·0)	−2·63 (6·3)
Xi19	−0·99 (11·7)	−2·31 (0·5)	−3·09 (0·0)	0·06 (52·4)	−2·07 (10·8)
d.f.	18	20	30	46	46
SED	0·633	0·832	0·838	0·492	1·522
F probability	0·046	0·698	0·066	0·279	0·262
Grand mean of back-transformed cultivar means	11·5	1·3	12·9	69·9	18·9

[a]High incidence of *Phialophora* spp.

[b]In 2004 cv. Avalon was sown late and the emerging seedlings were dislodged by feeding birds (rooks, *Corvus frugilegus*). As a consequence all the replicated plots established a very low overall plant density compared with other cultivars in the trial.

Table 4 Monthly rainfall (mm) and average maximum temperatures (°C) recorded at Rothamsted from May to August for the field seasons from 2004 to 2008 (data from the electronic Rothamsted Archive; e-RA)

Year	May	June	July	August	Total
Rainfall (mm)					
2004	52	32	50	113	247
2005	44	44	39	59	186
2006	89	15	36	110	250
2007	136	72	87	64	359
2008	87	35	90	108	320
Temperature (average t_{max} °C)					Mean
2004	16·3	20·3	21·4	22·4	20·1
2005	15·8	20·6	20·9	21·3	19·7
2006	16·4	21·6	26·1	20·3	21·1
2007	16·0	19·2	19·7	20·0	18·7
2008	18·0	18·8	20·9	20·1	19·5

the infectivity of the soil under these cultivars was highly significantly different ($P < 0·01$; Table 5). Consistent differences between cultivars were evident, with Cadenza ranked as a low builder, Riband a medium builder and Hereward at the high-building end of the scale. The difference in the percentage of roots infected in the soil core bioassay between Cadenza and Hereward was 44·4% over the 4 years, showing clearly the contrasting ability of these particular cultivars to build up take-all inoculum during a first wheat crop.

Discussion

The amount of inoculum in the soil at the time of sowing a susceptible crop greatly influences the amount of primary infection that occurs in that crop and so helps to determine final disease severity (Bailey & Gilligan, 1999). Much of the previous research on take-all inoculum has focused on the capability of other crops and grass weeds to maintain and carry over inoculum in a break year (Gutteridge *et al.*, 2006), the survival of Ggt inoculum in the field post-harvest (Macnish & Dodman, 1973; Bithell *et al.*, 2009), and how the length of the intercrop

Table 5 Mean percentage of roots infected in the soil core bioassay for nine winter wheat cultivars, grown as first wheat crops, sampled after harvest over 4 years of field experiments (2004, 2006, 2007 and 2008)[a]. REML variance components analysis was used to analyse differences between cultivars over all years

Cultivar	Logit % roots with take-all (back-transformed means)
Cadenza	−3·216 (3·4)
Xi19	−2·581 (6·6)
Mercia	−2·147 (10·1)
Riband	−2·019 (11·3)
Monopol	−1·613 (16·3)
Avalon	−1·336 (20·5)
Malacca	−1·202 (22·9)
Soissons	−1·108 (24·6)
Hereward	−0·086 (47·8)
Number of degrees of freedom	8
Denominator degrees of freedom	88·0
SED	0·781
Wald statistic	22·01
F probability	0·009

[a]2005 excluded from analysis due to the presence of competitive *Phialophora* spp.

period and environmental conditions influence inoculum decline in the soil (Colbach *et al.*, 1997; Gutteridge & Hornby, 2003). The results presented in this paper, however, suggest that there are potentially important differences between hexaploid wheats in their propensity to generate take-all inoculum.

The build-up of inoculum during a first wheat crop cannot be reliably simulated in pot or laboratory tests using field soil (R. Gutteridge, unpublished data). This makes investigating inoculum build-up reliant on field trials which are time consuming and vulnerable to variation in environmental conditions from year to year. Previous research has shown that the progression of take-all epidemics from build-up to TAD is significantly influenced by environmental conditions (Slope & Gutteridge, 1979; Bailey *et al.*, 2005; Pillinger *et al.*, 2005; Ennaifar *et al.*, 2007). High soil moisture levels have been associated with more severe take-all epidemics (Pillinger *et al.*, 2005). Conversely, delay in the onset of epidemics has been linked to cold weather (Bailey & Gilligan, 1999) which restricts mycelial growth and could also increase the rate of inoculum decay. Clearly environmental conditions have a considerable influence on the build-up of take-all inoculum in the soil and the progress of take-all epidemics. In 2007 and 2008, when conditions were most favourable for the build-up of inoculum, the effect of cultivar was less significant. Environmental conditions that are particularly conducive to the build-up of inoculum can also result in relatively high inoculum levels under even 'low building' cultivars. This reveals that favourable environmental conditions can mask cultivar effects to some extent. However, despite the complex relationship between the take-all fungus and environmental conditions, as well as the known difficulties in measuring take-all inoculum in the field due to uneven distribution and patchiness (Hornby, 1981), relatively consistent differences in the ability of wheat cultivars to build up take-all inoculum over the study period are reported here. This phenomenon has been named as the take-all inoculum build-up (TAB) trait.

The soil core bioassay measures the infectivity of the sampled soil. As described in the introduction, the degree of infectivity detected could potentially be due to a number of interacting factors, including the Ggt inoculum present, the type of soil microbial community present and/or the soil chemical properties which had each built up over the previous cropping period. In a previous study, a DNA-based detection test for Ggt was compared with the soil core bioassay at a range of infectivity levels and from two soil types (Gutteridge *et al.*, 2008). This comparative study revealed that a good correlation existed between DNA content of Ggt and the infectivity of the soil in two field experiments (linear regression $r = 0{\cdot}77$ and 0·79) with a moderate correlation in a third field experiment (linear regression $r = 0{\cdot}56$). In addition, recent field experiments in New Zealand have also shown a good relationship between the two methods (Bithell *et al.*, 2009). Based on these earlier results it is concluded that the soil core bioassay is predominantly measuring take-all inoculum build-up. However, it is acknowledged that the soil microbial community and/or the soil chemistries present in the collected soil sample could also influence the soil sample's infectivity in the subsequent bioassay. Post-collection, the soil samples are kept at 4°C and in the dark. This could successfully preserve different types of soil microbial communities and soil chemistries in addition to Ggt.

Excluding 2005, when *Phialophora* spp. were present, the results from the other 4 years suggest that opportunities may exist within current wheat germplasm to manipulate levels of natural take-all inoculum in the soil during a first wheat crop by appropriate choice of cultivar, and so reduce the risk of damaging disease occurring in the following, second, wheat crop. Limiting the build-up of inoculum during a first wheat crop could lead to more profitable second wheat crops and give farmers more freedom in choosing rotational cycles which contain a higher proportion of wheat crops. Yield differences between first and second wheats are typically 1–1·5 tonnes ha^{-1} (HGCA recommended list; http://www.hgca.com), and much of the yield difference is also considered to be directly attributable to the effect of take-all (Hornby *et al.*, 1998). When take-all is severe, yield differences can be even greater, so there is scope for a significant improvement in second wheat yields by minimising inoculum build-up in first wheats. The soil core bioassay method used here is time consuming and labour intensive and so is not suitable for commercial use. However, the newly developed DNA method (Ophel-Keller *et al.*, 2008) could provide a powerful tool for measuring inoculum build-up in the soil and disease risk which is quicker and more

suitable for commercial application. One problem with the DNA test is that it could overestimate the potential disease risk by detecting non infective, dead Ggt DNA. However, Gutteridge *et al.* (2008) have previously shown a good correlation between the amount of Ggt DNA measured using the DNA test and disease in the following second wheat crop, suggesting that the amount of non-infective take-all DNA found in field soils is low. If the correlation between the DNA level of take-all fungus in the soil and disease severity in the following crop could be confirmed in further locations/soils throughout the UK, the DNA test could be commercially useful to assess the risk of take-all in second wheat crops.

The mechanism(s) underlying cultivar differences in inoculum build-up reported here have not been established. It is not known whether the ability of a wheat cultivar to build-up inoculum as a first wheat crop is related to its susceptibility to take-all infection; historically only very small differences have been found between hexaploid wheat genotypes and their susceptibility to take-all in both field and pot tests (Scott, 1981; Freeman & Ward, 2004). Furthermore, first wheats can generate significant amounts of inoculum despite having few visible symptoms on the roots. Any mechanism(s) influencing inoculum build-up are therefore not likely to be related to the susceptibility of wheat cultivars to root infection by the take-all fungus. As discussed above, it is possible that wheat cultivars could influence the soil microbial community, perhaps as a result of differences in root exudates, root senescence and/or differences in root architecture affecting soil physical structure, and thus influence take-all inoculum survival and build-up. The occurrence of take-all decline (TAD), attributed to changes in the soil microbial community, is already well documented (Weller *et al.*, 2002) so it is known that take-all can be influenced by such changes in the soil.

The genetic basis of this phenomenon is also not yet known. The germplasm tested in these experiments was, genetically, highly diverse. The UK bread wheat cv. Hereward was consistently the highest take-all inoculum builder, although cvs Shamrock and Soissons were as, or more, effective in 2008. The consistently low building cultivars included the UK spring wheat Cadenza and both modern and semi-modern UK winter wheats with good grain quality characteristics, namely Xi19, Mercia and Riband. Xi19 is one of the highest yielding UK bread wheats and is closely related to another of the consistently low building cultivars, Cadenza (Xi19 pedigree: (Cadenza × Rialto) × Cadenza; http://www.nickerson seeds.co.uk). The Cadenza pedigree is also present in Cordiale ((Reaper × Cadenza) × Malacca; http://www.kws-uk.com), a low to medium building cultivar sampled in three of the five WGIN trial years. Other low and medium building cultivars such as Mercia and Riband have pedigrees unrelated to Cadenza, Cordiale and Xi19. This suggests the existence of a range of genetically diverse germplasm conferring the low TAB trait, which could be used in breeding programmes if further research demonstrates that it has potential value in take-all disease management programmes under commercial conditions.

Further work is now required to investigate the significance of the finding reported here. A number of studies have previously correlated the percentage of roots infected in the soil core bioassay with disease in the field in the following crop (Hornby *et al.*, 1998; Gutteridge *et al.*, 2008; Bithell *et al.*, 2009). In further field trials more information could be gained by measuring take-all in second wheat crops after different first wheat cultivars. It would then be possible to determine whether the differences in inoculum build-up reported here could be of real value to help minimize disease in the following crop. Within the continuing WGIN project, wheat cultivar rotational studies have already commenced to explore whether particular combinations of first and second wheat cultivars maximize or minimize disease levels in second wheat crops.

Also, although there are a number of studies on inoculum decline between harvest and sowing in relation to the length of the inter-crop period and environmental conditions (Macnish & Dodman, 1973; Slope & Gutteridge, 1979; Wong, 1984; Colbach *et al.*, 1997; Gutteridge & Hornby, 2003; Bithell *et al.*, 2009), it is not known if the conditions created or mechanisms involved in differential inoculum build-up between wheat cultivars could result in changes to the rate of inoculum decline between harvest and sowing. It is possible that such differences could influence the disease outcome in the second wheat crop.

Further research and field trials could also indicate whether it is possible to speed up take-all epidemics and the natural build-up of suppressive soils in consecutive wheat crops (take-all decline). TAD describes the reduction in take-all disease in consecutive wheat crops after a peak of take-all is reached in the 2nd to 4th years (Slope & Cox, 1964). It is perhaps possible that by selecting a high building cultivar as a first wheat, peak levels of take-all disease could be established more quickly and the soil pushed into decline over fewer seasons so that farmers could benefit when their intention is to grow consecutive wheat crops in the long term.

Although the genetic or mechanistic basis of this phenomenon is not yet known, the use of different cultivars to manipulate inoculum levels in the soil could provide farmers with a practical solution to reduce the risk of damaging take-all disease in second wheat crops.

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References

Bailey DJ, Gilligan CA, 1999. Dynamics of primary and secondary infection in take-all epidemics. *Phytopathology* **89**, 84–91.

Bailey DJ, Paveley N, Pillinger C, Foulkes J, Spink J, Gilligan CA, 2005. Epidemiology and chemical control of take-all on seminal and adventitious roots of wheat. *Phytopathology* **95**, 62–8.

Barraclough PB, Howarth JR, Jones J *et al.*, 2010. Nitrogen efficiency of wheat: genotypic and environmental variation and prospects for improvement. *European Journal of Agronomy* **33**, 1–11.

Bithell SL, Mclachlan ARG, Hide CCL, Mckay A, Cromey MG, 2009. Changes in post-harvest levels of *Gaeumannomyces graminis* var. *tritici* inoculum in wheat fields. *Australasian Plant Pathology* **38**, 277–83.

Colbach N, Lucas P, Meynard JM, 1997. Influence of crop management on take-all development and disease cycles on winter wheat. *Phytopathology* **87**, 26–32.

Cook RJ, 2003. Take-all of wheat. *Physiological and Molecular Plant Pathology* **62**, 73–86.

Ennaifar S, Makowski D, Meynard JM, Lucas P, 2007. Evaluation of models to predict take-all incidence in winter wheat as a function of cropping practices, soil, and climate. *European Journal of Plant Pathology* **118**, 127–43.

Freeman J, Ward E, 2004. *Gaeumannomyces graminis*, the take-all fungus and its relatives. *Molecular Plant Pathology* **5**, 235–52.

Gutteridge RJ, Hornby D, 2003. Effects of sowing date and volunteers on the infectivity of soil infested with *Gaeumannomyces graminis* var. *tritici* and on take-all disease in successive crops of winter wheat. *Annals of Applied Biology* **143**, 275–82.

Gutteridge RJ, Jenkyn JF, Bateman GL, 2006. Effects of different cultivated or weed grasses, grown as pure stands or in combination with wheat, on take-all and its suppression in subsequent wheat crops. *Plant Pathology* **55**, 696–704.

Gutteridge RJ, Treskic S, Hammond-Kosack KE, 2008. *Assessing Take-all Risk in Second Wheats using the Predicta B Test*. London, UK: Home-Grown Cereals Authority: HGCA Project Report No. 445.

Hornby D, 1981. Inoculum. In: Asher MJ, Shipton PJ, eds. *Biology and Control of Take-all*. London, UK: Academic Press, 271–94.

Hornby D, 1983. Suppressive soils. *Annual Review of Phytopathology* **21**, 65–85.

Hornby D, Bateman GL, Gutteridge RJ *et al.*, 1998. *Take-all Disease of Cereals: A Regional Perspective*. Wallingford, UK: CAB International.

Lebreton L, Gosme M, Lucas P, Guillerm-Erckelboudt AY, Sarniguet A, 2007. Linear relationship between *Gaeumannomyces graminis* var. *tritici* (*Ggt*) genotypic frequencies and disease severity on wheat roots in the field. *Environmental Microbiology* **9**, 492–9.

Macnish GC, Dodman RL, 1973. Survival of *Gaeumannomyces graminis* var. *tritici* in the field. *Australian Journal of Biological Sciences* **26**, 1309–17.

Ophel-Keller K, Mckay A, Hartley D, Herdina MKK, Curran J, 2008. Development of a routine DNA-based testing service for soilborne diseases in Australia. *Australasian Plant Pathology* **37**, 243–53.

Pillinger C, Paveley N, Foulkes MJ, Spink J, 2005. Explaining variation in the effects of take-all (*Gaeumannomyces graminis* var. *tritici*) on nitrogen and water uptake by winter wheat. *Plant Pathology* **54**, 491–501.

Scott PR, 1981. Variation in host susceptibility. In: Asher MJC, Shipton PJ, eds. *Biology and Control of Take-all*. London, UK: Academic Press, 219–36.

Shipton PJ, 1981. Saprophytic survival between susceptible crops. In: Asher MJC, Shipton PJ, eds. *Biology and Control of Take-all*. London, UK: Academic Press, 295–315.

Skou JP, 1981. Morphology and cytology of the infection process. In: Asher MJC, Shipton PJ, eds. *Biology and Control of Take-all*. London, UK: Academic Press, 175–98.

Slope DB, Cox J, 1964. Continuous wheat growing and the decline of take-all. In: *Rothamsted Experimental Station Report for 1963*. Bungay, UK: Richard Clay and Co., Ltd, 108.

Slope DB, Gutteridge RJ, 1979. Epidemiology of take-all. In: *Rothamsted Experimental Station Report for 1978*. Dorking, UK: Adlard & Son Ltd., Bartholomew Press, 215.

Slope DB, Prew RD, Gutteridge RJ, Etheridge J, 1979. Take-all, *Gaeumannomyces graminis* var. *tritici*, and yield of wheat grown after ley and arable rotations in relation to the occurrence of *Phialophora-radicicola* var. *graminicola*. *Journal of Agricultural Science* **93**, 377–89.

Walker JL, 1981. Taxonomy of the take-all fungi and related genera and species. In: Asher MJC, Shipton PJ, eds. *Biology and Control of Take-all*. London, UK: Academic Press, 15–74.

Weller DM, Raaijmakers JM, Gardener BBM, Thomashow LS, 2002. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annual Review of Phytopathology* **40**, 309–48.

Widdowson FV, Penny A, Gutteridge RJ, Darby RJ, Hewitt MV, 1985. Tests of amounts and times of application of nitrogen and of sequential sprays of aphicide and fungicides on winter wheat, following either beans or wheat, and the effects of take-all (*Gaeumannomyces graminis* var *tritici*), on two varieties at Saxmundham, Suffolk 1980–3. *Journal of Agricultural Science* **105**, 97–122.

Wong PTW, 1984. Saprophytic survival of *Gaeumannomyces graminis* and *Phialophora* spp. at various temperature-moisture regimes. *Annals of Applied Biology* **105**, 455–61.

Yarham DJ, 1981. Practical aspects of epidemiology and control. In: Asher MJC, Shipton PJ, eds. *Biology and Control of Take-all*. London, UK: Academic Press, 353–85.