European Journal of Plant Pathology (2005) 112: 167–181
DOI: 10.1007/s10658-005-3121-8

Effects of summer fallow management on take-all of winter wheat caused by *Gaeumannomyces graminis* var. *tritici*

S. Ennaïfar[1], P. Lucas[2], J.-M. Meynard[3] and D. Makowski[1]
[1]*UMR d'Agronomie INRA/INA P-G, BP01, 78850 Thiverval-Grignon, France; (Fax: +33-130-815425; E-mail: ennaifar@grignon.inra.fr);* [2]*UMR BIO3P INRA-Agrocampus, Domaine de la Motte, BP 35327, 35653 Le Rheu Cedex, France;* [3]*Département SAD, BP01, 78850 Thiverval-Grignon, France*

Accepted 3 March 2005

Key words: conventional tillage, monoculture, no-tillage, silthiofam, wheat volunteers

Abstract

Crop rotation is the oldest, and perhaps the best cultural practice for reducing the risk of take-all. The effects of crops sown before wheat in a rotation are known in detail, but we know little about the opportunities for reducing take-all risk by planting certain crops in the summer period between wheat harvest and the planting of a subsequent winter wheat crop. We investigated the effects on take-all of five summer fallow crops, two soil tillage treatments and a fungicide seed treatment, in a five site-year experiment. We tested the effects of oats, oilseed rape, mustard, ryegrass and volunteer wheat crops. Bare-soil plots were also included. Take-all epidemics varied with year and site. Summer fallow crops had a greater effect on tilled plots. The incidence and severity of take-all were significantly higher in the wheat volunteer plots, whereas maintaining bare soil provided the lowest level of disease. Oilseed rape had no significant effect on take-all incidence in our experiment. The best candidates for reducing take-all risk appeared to be oats, mustard and ryegrass. These summer fallow crops decreased disease levels only when associated with conventional tillage. Summer fallow crops did not alter take-all decline in the same way as a break crop after a wheat monoculture.

Abbreviations: AUDPC – area under the disease progress curve; Ggt – *Gaeumannomyces graminis* var. *tritici*; GLM – generalised linear model; Gri201, Gri601, Gri702, LR202 and LR203 – field experiment codes (Gri for Grignon and LR for Le Rheu, followed by the order of the assessed wheat crop [2 for second wheat crop, 6 for sixth wheat crop or 7 for seventh wheat crop] and the harvest year [2001, 2002, or 2003]); GS – Zadoks growth stage; GS 15 – 5 leaves unfolded; GS 30 – pseudostem elongation; GS 32–33 – mid-stem elongation; GS 65 – flowering; GS 89 – ripening; F+/F− – with/without fungicide seed treatment; Till/no-till – conventional tillage/direct drilling.

Introduction

Take-all on winter wheat is caused by *Gaeumannomyces graminis* var. *tritici* (Ggt). This disease has been extensively studied (Hornby et al., 1998), deepening our understanding of the mechanisms governing its development. This soil-borne fungus develops on both wheat and barley. None of the various cultural (Colbach, 1995; Colbach et al., 1997), biological (Wong, 1975; Simon and Sivasithamparam, 1988; Cook, 1994) and chemical (Schoeny and Lucas, 1999) control methods have proved sufficiently effective to prevent yield losses (Schoeny et al., 2001). Crop rotations constitute a powerful strategy against the development of this pathogen

(Lemaire and Coppenet, 1968; Cook, 1981; Kollmorgen and Walsgott, 1983; Cotterill and Sivasithamparam, 1988;). The crops of the rotation may be classified, on the basis of their susceptibility or their effects on the pathogen, as host crops, non-host crops or amplifying crops (Colbach et al., 1994). A non-host crop reduces the Ggt population to levels guaranteeing the economic viability of subsequent wheat or barley crops (Werker et al., 1991). The use of non-host crops such as linseed (*Linum usitatissimum*) (Kirkegaard et al., 1997), black medic (*Medicago lupulina*), beans (*Vicia faba*) (Prew and Dyke, 1979), spring peas or oilseed rape (McEwen et al., 1989), none of which are cereals, or of oats, eliminates take-all disease or reduces its incidence in subsequent host crops.

In France, rotations for lowering take-all risk face two challenges: the low economic value of some break crops and the predominance of wheat and barley (6.33 M ha) (Scees, 2003; Ministère de l'Agriculture and www.agpb.fr) within areas subject to crop rotation (13.5 M ha including 3.27 M ha maize, which is considered to be an amplifying crop for take-all) (Colbach et al., 1994). Most studies on crop rotations have focused on cash crops in the soil for several months. Little is known about the effects of introducing these crops into the rotation for a short period of time – during the summer fallow for instance – not for production purposes, but to meet environmental criteria. These criteria relate to the nutrient supply and soil nitrogen trapping (McEwen et al., 1989), improvement of the physical characteristics of the soil, and improving the control of erosion and pest control (Rothrock and Langdale, 1989). These crops must belong to non-susceptible species and must not harbour pathogens that might harm the subsequent crop. Other effects may also be considered, including the allelopathic effects of some crops in particular. The first studies carried out in this domain focused on the control of weeds rather than diseases (Bullock, 1992), but recent studies have shown that residues of *Brassica* crops may eliminate soil-borne pathogens by means of biocidal components, such as isothiocyanates (Kirkegaard et al., 2000). Isothiocyanates are generated by the hydrolysis of glucosinolates within plant tissues; they inhibit weed seed germination (Brown and Morra, 1995), and the development of soil-borne pathogens such as *Rhizoctonia* spp., *G. graminis* (Brown and Morra, 1997), and nematodes such as *Pratylenchus neglectus* (Potter et al., 1998). Glucosinolates may have very different, heterogeneous effects. Mazzola et al. (2001) observed that populations of *Pythium* spp. were activated by the addition of low levels of glucosinolates.

Another cropping system factor influencing disease development is soil tillage. The effect of tillage depends on the rotation (Colbach and Meynard, 1995). The two crops immediately preceding the crop considered in the rotation and soil tillage together determine the position of infectious residues in the soil profile. In the face of economic and environmental challenges, there is currently a trend in France towards the simplification of farming practices and conservation tillage, including no-tillage or direct drilling practices (Guérif, 1991). Weeds abound in conservation tillage systems, hindering plant growth and decreasing yields. The chemical control of weeds is therefore essential to the success of the system.

Ggt does not spread rapidly in the soil in the absence of a host, but it can survive for at least one year in the soil, on the residues of previous crops. With direct drilling, residues are not well mixed throughout the soil profile, limiting the spread of the fungus in the soil and therefore also its radius of contamination (Rothrock, 1987). However, by keeping large crop residues on the soil surface, direct drilling modifies the physical and chemical conditions of the profile and the aeration of the soil, affecting the activity of the fungus. Direct drilling decreases the rate of decomposition of organic matter in the soil as microbial populations decrease in size below a depth of 7.5 cm (Doran, 1980). This in turn protects the fungus, ensuring its survival on undecomposed residues. Tillage increases microbial activity in the soil, accelerating the decay of soil organic matter, including the refuges of *G. graminis* (Bockus and Shroyer, 1998). This may also lead to an increase in parasitism and nutrient competition at the rhizosphere level (Lockwood, 1986), affecting the colonisation of the roots by this weakly pathogenic, primarily saprophytic fungus.

During continuous wheat cropping, the inhibition of the take-all fungus observed in a period of decline may be related to the stimulation of an antagonistic microflora composed of bacteria, such as fluorescent *Pseudomonas* spp. (Weller and Cook, 1983; Brisbane and Rovira, 1988; Sarniguet et al., 1992b). Studies in France have shown that black-grass volunteers (*Alopecurus myosuroides*) present in set-aside fields maintain the endogenous take-all inoculum without stimulating the development of this antagonistic microflora as for wheat volunteers (Dulout et al., 1997). Fallow periods are introduced into rotations to facilitate the cleaning and regeneration of the soil. However, these observations demonstrate the importance of fallow management (through weed control and canopy destruction). This is confirmed by the low indices of take-all measured following bare soil (Dulout et al., 1997). Similar results have been obtained for systems with permanent cover crops, such as fescue (*Festuca rubra*), which enables Ggt to maintain and to develop its populations (Picard et al., 2000). The effects of crops preceding wheat in the rotation are well known, but we know little about the opportunities for reducing take-all risk except for introducing certain crops into the rotation during the summer period between wheat harvest and the subsequent winter wheat crop, as cultural control strategies against take-all. We also know little about the interactions between these crops and tillage practices before the main crop is established.

In this study, we carried out field experiments to investigate the effects of six summer canopies and of two tillage practices on the development of take-all epidemics in the subsequent winter wheat crop, and on winter wheat yield. We analysed the interaction between summer fallow crop and soil tillage practices for residue management in the presence and absence of a fungicide seed treatment against take-all.

Materials and methods

Field experiment

We carried out five trials in three cropping seasons (2000–2001, 2001–2002 and 2002–2003) at two sites: one in the Parisian area (Grignon) and one in Brittany (Le Rheu). Trials were coded with the initials of the location (Gri for Grignon or LR for Le Rheu) followed by the order of the assessed wheat crop in the rotation and the year of harvest. The experimental fields were chosen such that their cropping histories were different, presumably resulting in different initial levels of inoculum. Three fields had only one winter wheat crop preceding the assessed winter wheat crop, giving a high take-all risk (LR202, LR203, Gri201). One of the other fields was under continuous wheat,

Table 1. Description of the field experiments (experimental design, cropping history, years of planting, and treatments) used to assess the effect of summer fallow management on take-all of winter wheat in France in 2000–2003

	Experiment				
	Gri201	Gri601	Gri702	LR202	LR203
Cropping history, year of planting, and treatment					
Recent cropping history[a]	f–ww–wb–r–ww	5-year wheat	6-year wheat	ww–ww–m–ww	ww–ww–ww–m–ww
Year of experiment	2001	2001	2002	2002	2003
Summer fallow canopies	2 treatments[b]	2 treatments[b]	6 treatments[c]	6 treatments[c]	6 treatments[c]
Soil tillage treatment	Till/no-till	Till/no-till	Till/no-till	Till/no-till	Till/no-till
Seed-treatment	None	None	None	Silthiofam	Silthiofam
Description of the field experiments					
Sowing date	25 Oct. 2000	25 Oct. 2000	11 Oct. 2001	15 Oct. 2001	29–31[d] Oct. 2002
Number of blocks	2	2	2	2	2
Plot size	13.5 m × 8 m	13.5 m × 8 m	12 m × 4.5 m	12 m × 12 m	12 m × 8 m
Number of sampling dates	5	5	5	5	5
Number of samples per date	4	4	4	4	4
Sample size	50 cm × 2 rows	50 cm × 2 rows	25 cm × 2 rows	25 cm × 2 rows	25 cm × 2 rows

ww, winter wheat; f, fallow; wb, winter barley; r, oilseed rape; m, maize.
[a]Crops preceding the winter wheat crop studied.
[b]Bare soil, mustard.
[c]Bare soil, mustard, oats, oilseed rape, ryegrass and wheat volunteers.
[d]Till and no-till, respectively.

resulting in low take-all risk because of take-all decline (Gri601, Gri702) (Table 1).

The three experimental factors considered were (i) summer fallow crops sown after harvesting of the previous wheat crop: two treatments for Gri201 and Gri601 (mustard and bare soil) and six treatments for Gri702, LR202 and LR203 (oats (cv. Ourasi), ryegrass (cv. Ohio), oilseed rape (cv. Lutin), mustard (cv. Carnaval), wheat volunteers (cv. Cézanne) and bare soil); (ii) soil tillage: two treatments for the five trials (conventional tillage, till and direct drilling, no-till) and (iii) seed treatment with the fungicide silthiofam (Latitude® from Monsanto Agriculture SAS), for the Rheu trials only, applied at a rate of 25 g a.i./100 kg of seed (F+) *versus* non-treated seeds (control, F−). The experimental treatment is the combination of the various treatments.

Implementation of the factorial experimental design was facilitated by making use of a strip-block with two or three experimental factors and two blocks. Each block was divided into two strips in one direction, to which the tilling practices were attributed at random. Each individual strip was further subdivided into two substrips, to which fungicide treatments were assigned at random. Perpendicularly, each block was divided into six strips, to which summer fallow crops were randomly assigned. The size of the plot depended on the trial (Table 1).

For all trials, a stubble break preceded the broadcast sowing of the summer fallow crop, at the beginning of August each year. This was followed by the use of a crosskill roller to firm the land at depth. Bare soil plots were maintained by glyphosate (Roundup®; 5.5 l ha^{-1}; Monsanto Agriculture SAS) application to control weeds. In LR202, the other plots were treated with Paraquat (Gramoxone®; 3.5 l ha^{-1}; Syngenta Agro). Two months after sowing, canopies were destroyed by grinding or mowing. For establishment of the subsequent winter wheat crop, seedbed preparation consisted of ploughing and circular spike-harrowing for conventional tillage. The winter wheat crop was sown with a shoe drill. For direct drilling, winter wheat was sown with a disc drill at the Grignon site. At Le Rheu, for the no-till treatment, winter wheat was sown using a direct drill. We used a sowing density of about 300 seeds per m^2 for all trials. We used the following wheat cultivars: Cézanne in 2001, Apache in 2002 and Caphorn in 2003. Nitrogen fertiliser was applied twice, uniformly over each site. We applied ammonium nitrate (33.5% N) at a rate of 160 kg ha^{-1} in 2001 and 130 kg ha^{-1} in 2002 at Grignon and ammonium solution (34% N) at a rate of 120 kg ha^{-1} at Le Rheu in two experiment years. Weeds, foliar and stem diseases and aphid populations were maintained below threshold levels, as recommended in "les Avertissements Agricoles du Service de la Protection des Végétaux".[1]

Sampling and disease assessment

Take-all was assessed at five growth stages: GS 15 (five leaves unfolded), GS 30 (pseudostem elongation), GS 32-33 (2nd and 3rd node detectable), GS 65 (flowering) and GS 89 (ripening) for all experiments except LR203, for which only four stages were considered (Table 2) (Zadoks et al., 1974). In 2002 and 2003, four samples, 25 cm long, over two rows, were taken from each plot at each sampling date. Ten plants from each sample were randomly chosen for disease assessment. In 2001, we took 50 cm long samples over the two rows and 20 plants per sample were assessed. Immediately after sampling, the root systems were washed to remove adhering soil and assessed. If assessments could not be made immediately after washing, the plants were kept in a cold chamber at a temperature not exceeding 5 °C. Two variables were used for disease assessment: (a) incidence, corresponding to the percentage of plants assessed that were diseased; (b) severity, graded on a scale from 0 to 100 per quanta of 10 (Lucas et al., 1989), expressing the proportion of the root system showing symptoms (black stelar discolouration). Both root systems (seminal and nodal) were assessed separately before tillering, whereas only the nodal root system was assessed after tillering.

We also carried out the following measurements: density of summer fallow crops (quantitative observations) and dry matter determination for summer fallow crops. These measurements were made at Gri702 before the removal of the summer fallow crops, providing an estimate of the abundance of wheat volunteers and of the sown canopy.

[1]Anon. (2003) Bulletins Techniques des Stations d'Avertissements Agricoles n° 4 à 13. http://draf.bretagne.agriculture.gouv.fr.

Table 2. Correspondence between calendar dates, cumulative days and degree-days since sowing, and growth stage of plants at the time of sampling for field experiments conducted in France in 2000–2003

Sampling time	1	2	3	4	5
Gri201 and Gri601					
Date	13 Feb.	26 Mar.	23 Apr./25	22 May	1 Jul.
Days since sowing	111	152	180/182[a]	209	249
Degree-days since sowing	786	1070	1305/1327[a]	1675	2356
Growth stage[c]	15	30	32	51	73
Gri702					
Date	29 Jan.	25 Mar.	19 Apr.	24 May	25 Jun.
Days since sowing	110	165	190	225	257
Degree-days since sowing	752	1205	1432	1876	2406
Growth stage[c]	15	30	33	65	89
LR202					
Date	25 Jan.	16 Mar.	28 Mar.	24 May	19 Jun.
Days since sowing	102	142	164	221	247
Degree-days since sowing	754	1100	1323	1973	2373
Growth stage[c]	15	30	33	65	89
LR203					
Date	11 Feb.	–	1 Apr.	20 May	18 Jun.
Days since[d]	103/105	–	152/154	201/203	230/232
Degree-days since sowing[b]	785/809	–	1205/1228	1779/1803	2280/2304
Growth stage[c]	15	–	33	59	83

–, no sampling.
[a]The first value corresponds to Gri601, and the second to Gri201.
[b]Base 0 °C.
[c]Decimal wheat growth stage (Zadoks et al., 1974).
[d]The first value corresponds to no tillage and the second to conventional tillage.

Assessment of yield components

We sampled plants at maturity to estimate yield components (except for Gri702 trial). We used the same sampling method described above except that plants were cut above ground level because disease assessment was no longer necessary. Plants were sampled from the two rows left untouched for harvest. Ears were cut, counted, placed in a drying chamber for 48 h at 70 °C and threshed. Grains were dried a second time, for 24 h at 70 °C, and were then weighed and counted with an electronic seed counter. Finally, ear number per m^2, grain number per ear, grain number per m^2, 1000-grain weight at 16% water content, and grain yield at 16% water content were estimated.

Statistical analysis

Trials were carried out in different sites and years. For this reason, incidence data for each treatment in each experiment were first analysed jointly for all sampling dates in order to characterise differences between experiments that may be attributed to the field cropping history or the environment. Take-all progress curves were determined by fitting a non-linear model to the incidence data for each experiment, experimental treatment and block (Colbach and Meynard, 1995; Colbach et al., 1997). The model included two parameters, c_1 and c_2 associated with primary and secondary infections, respectively, according to the following equation:

$$y(t) = \frac{1 - e^{-(c_1+c_2)t}}{1 + \left(\frac{c_2}{c_1}\right) e^{-(c_1+c_2)t}}$$

where t is the independent variable used to represent thermal time in cumulative degree days (basis 0 °C) and $y(t)$ is the disease incidence at time t. The non-linear model (NLIN) procedure of SAS was used, applying weighted least squares with the reciprocal of error variances corresponding to each assessment stage as weights. An iterative algorithm provides estimates of c_1 and c_2 for each experimental treatment of each block. The estimates $\hat{c}_1$ and $\hat{c}_2$ made it possible to calculate the incidences predicted by the model, used for the calculation of an additional disease variable – the area under the disease progress curve (AUDPC) – according to the formula:

$$\mathrm{AUDPC}_{S_1,S_2} = \sum_{t=S_1}^{t=S_2-dt} \frac{[y(t) + y(t+dt)]}{2} dt$$

where $y(t)$ is disease incidence at time t (expressed in degree days, basis 0 °C), dt is the time interval, set to 1, and S_1 and S_2 are the growth stages (in degree days, basis 0 °C) for which the AUDPC is calculated (Schoeny et al., 2001). Only the AUDPC calculated between sowing and flowering were taken into account in subsequent analyses.

To characterise the effects of the experimental treatments on the disease variables, data were also analysed separately for each experiment and sampling date. We assessed the homogeneity of variances. When necessary, disease data were transformed by the square root arcsine transformation for analysis and transformed back for presentation. Using the generalised linear model (GLM) procedure of the SAS software package (SAS Institute, 1989), a separate analysis of variance for each experiment, with three main factors (soil tillage, summer fallow crop and fungicide), their interactions, and block effects was performed for each trial and sampling date, on all disease variables and yield components. Each source of variation was compared to its interaction with the block factor as residual term. Due to the small number of replicates (two blocks), and considering the patchy distribution of take-all, we treated samples taken from each plot as internal replicates. Means for main effects were compared using the Student–Newman–Keuls test. The standard error of the difference (SED) between the mean levels of each factor was estimated by taking the square root of the respective error mean square. Contrasts (specified with the CONTRAST and ESTIMATE statements of the SAS software) were used to test the significance of differences between summer fallow crops for given treatments of soil tillage and fungicide, particularly when significant interactions were found.

Results

Characteristics of the summer fallow crops

At Gri702, quantitative observations were used to estimate the abundance of wheat volunteers on every plot and the establishment of summer fallow crops. Wheat volunteers and mustard had the highest (P < 0.05) shoot weights (109 and 130 g m^{-2}, respectively). Ryegrass and oats had a high plant density (210 and 87 plants m^{-2} i.e. 18 and 27 g m^{-2}, respectively) but wheat volunteers developed well (131 and 101 wheat plants m^{-2}, respectively, *versus* 45 plants m^{-2} for mustard, which grew rapidly, shading weeds and wheat volunteers, thereby reducing their growth and density). Oilseed rape developed well (43 g m^{-2}) but was infested with wheat volunteers (54 wheat plants m^{-2} i.e. 46 g m^{-2}). In the Grignon 2001 trials, mustard canopies were homogeneous and dense. The number of wheat volunteers on the bare soil plots Gri601 and Gri201 was similar to that on the wheat volunteer plots Gri702. We therefore considered the bare plots as equivalent to a wheat volunteers treatment at Gri201 and Gri601. Plants were not counted in the Le Rheu trials. Qualitative observations showed a homogeneous and dense canopy for oilseed rape, oats, and mustard, and a homogeneous but not very dense canopy for ryegrass. The bare soil in the Le Rheu trials was well maintained by herbicides (see Materials and methods).

Take-all epidemics depended on site and year

Take-all epidemics varied in earliness and amplitude among the various summer fallow crop–soil tillage–fungicide treatment combinations. Figure 1 shows, for each trial, disease incidence for a given treatment combination of the three experimental factors, with wheat volunteers followed by conventional tillage in plots without fungicide. At Le Rheu, epidemics according to disease incidence developed early, spread rapidly and resulted in very high levels of take-all during much of the cropping season in each experimental year. Disease was particularly severe during the 2003 cropping season. Disease was so high in the LR203 trial that some plants on some plots died prematurely. For this reason, we did not sample direct-drilled and untreated plots after the mid-stem elongation growth stage. At Le Rheu, the incidence on untreated plots

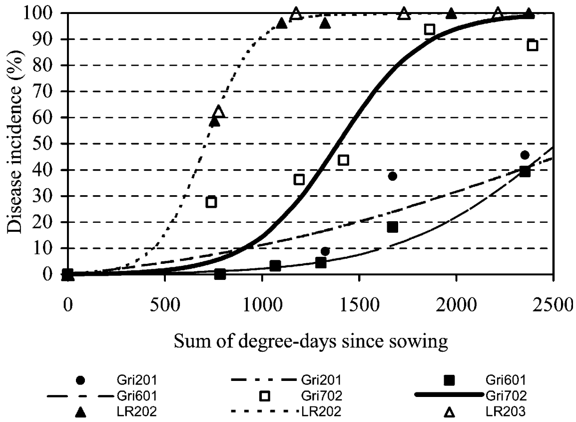

Figure 1. Take-all progress curves in untreated wheat plots for the five field experiments with wheat volunteers followed by conventional tillage. Symbols represent observed means of disease incidence for each experimental site and assessment date. Take-all was assessed at five growth stages: GS 15 (five leaves unfolded), GS 30 (pseudostem elongation), GS 32-33 (2nd and 3rd node detectable), GS 65 (flowering) and GS 89 (ripening) for all experiments except LR203, for which only four stages were considered (Zadoks et al., 1974). Lines are fitted curves (from sowing to harvest). No progress curve was fitted to disease data from LR203 for this experimental treatment.

varied between 40% and 90% on seminal roots at GS 15, and between 90% and 100% on nodal roots at GS 65. Take-all epidemics according to disease severity occurred later and increased slowly until flowering. Severity was in the range of 5–20% on seminal roots at GS 15 and in the range of 30–90% on nodal roots at GS 65. Finally, a disease incidence of 100% was observed for almost all the treatments at the end of the cropping season.

Epidemics were milder at Grignon than at Le Rheu, and differed from year to year. In the 2001 cropping season, take-all epidemics developed late and had almost no effect. During the 2002 cropping season, a moderate to strong epidemic occurred (disease incidence of 7–34% at GS 15, reaching 65–94% at GS 65, on nodal roots). At this site with a long history of wheat monoculture, incidence was higher than that for Gri601, but severity was low, with less than 4% diseased roots at GS 15, and no more than 40% diseased roots by the end of the cropping season.

Tables 3 and 4 summarise the epidemics in terms of area under disease progress curves (AUDPC) calculated from the disease incidence variable for each block of each experimental treatment and trial. This variable confirms the results reported above, with disease level differing considerably with site, experiment year, cropping history and experimental factors: AUDPC at Le Rheu trials varied between 475 and 1328 and that at Grignon varied between 43 and 203 in 2001 and between 264 and 692 in 2002.

Treatment effects on take-all epidemics

The insertion of short-duration summer crops into a winter wheat rotation had significant effects on disease variables, on seminal roots (results not shown) in the first instance, and then on nodal roots, depending on sampling time and trial. Schoeny et al. (2001) have shown that disease levels assessed at mid-stem elongation in a series of trials carried out at Le Rheu account for the yield losses caused by take-all. Based on this result, only disease data obtained at GS 32-33 were reported in subsequent analyses.

For LR202, the summer fallow crop had a significant effect ($P < 0.05$) at GS 33 and soil tillage had a small effect ($P = 0.06$) on incidence and no effect on severity (Table 5), but the interaction between these two factors was significant ($P < 0.01$), for both the incidence and severity of take-all. The effects of summer fallow crops therefore depended on soil tillage practices before the establishment of the main crop. Fungicide treatment reduced significantly ($P < 0.01$) disease levels at GS 33 (Table 5), and this effect was apparent in both incidence and

Table 3. Area[a] under the disease progress curve between sowing and flowering for each experimental treatment at Le Rheu

	LR202[b]				LR203			
	Till		No-till		Till		No-till	
Summer fallow canopy	F–	F+	F–	F+	F–	F+	F–[c]	F+
Oats	914	635	1235	870	1020	890	–	878
Volunteers	1261	1013	1254	894	–[d]	872	–	902
Oilseed rape	1249	844	1113	775	994	762	–	790
Mustard	1095	959	1310	944	932	829	–	725
Ryegrass	1018	899	1328	898	983	958	–	885
Bare soil	1060	475	1121	700	905	711	–	657
SED[e]	147 (24 df)							
Means (fungicide)	1100	804	1227	847	–	836	–	806
SED[f]	60 (24 df)				32 (16 df)			
Means (tillage)	952		1037		–		–	
SED[g]	42 (24 df)							
Means (experiment)	994				–			

–, data not determined; SED, standard error of difference; df, degrees of freedom; F-, untreated plots; F+, treated plots (seed treatment: 25 g a.i./100 kg seed).
[a]Values are means of two blocks.
[b]Significant effects of the fungicide ($P = 0.0001$), the summer fallow canopy ($P = 0.01$) and the soil tillage ($P = 0.05$) treatments on the AUDPC for LR202.
[c]Not determined because of premature death of plants in this treatment.
[d]Not calculated because no curve was fitted for this treatment.
[e]Value indicates standard error of difference for comparison among all treatments.
[f]Value indicates standard error of difference for comparison among all soil tillage and fungicide treatments.
[g]Value indicates standard error of difference for comparison between soil tillage treatments.

severity. We were particularly interested in comparing the effects of the various summer fallow crops with those of wheat volunteers (corresponding to the most common farm practice during summer fallow), under all combinations of the other treatments. For LR202, significant differences ($P \leq 0.01$) in disease incidence and severity at GS 33 were found be-

Table 4. Area[a] under the disease progress curve between sowing and flowering for each experimental treatment at Grignon

Summer fallow canopy	Gri201		Gri601		Gri702[b]	
	Till	No-till	Till	No-till	Till	No-till
Oats	–	–	–	–	476	646
Volunteers	155	95	43	89	468	692
Oilseed rape	–	–	–	–	600	625
Mustard	203	177	140	118	404	438
Ryegrass	–	–	–	–	679	551
Bare soil	–	–	–	–	264	331
SED[c]	62 (4 df)		60 (4 df)		117 (12 df)	
Means (tillage)	179	136	92	104	482	574
SED[d]	44 (4 df)		42 (4 df)		48 (12 df)	
Means (experiment)	158		98		514	

–, not tested; SED, standard error of difference; df, degrees of freedom.
[a]Values are means of two blocks.
[b]Significant effect of the summer fallow canopy ($P = 0.01$) on the AUDPC for Gri702.
[c]Value indicates standard error of difference for comparison among all treatments.
[d]Value indicates standard error of difference for comparison between soil tillage treatments.

Table 5. Effects of summer fallow canopies, soil tillage and fungicide on take-all incidence[a] and severity[a] on nodal roots in the five field experiments, at mid-stem elongation (GS 32-33)

Experimental factor	Experiment							
	Gri201	Gri601	Gri702		LR202		LR203[b]	
	Incidence	Incidence	Incidence	Severity	Incidence	Severity	Incidence	Severity
Summer fallow canopy								
Oats	–	–	42 (44)	13.5 (5)	55 (67)	21 (13)	89 (100)	36 (35)
Volunteers	14 (6)	12 (5)	51 (60)	16 (8)	70 (88)	29 (24)	84 (99)	41 (42)
Oilseed rape	–	–	42 (44)	13 (5)	66 (83)	26 (19)	89 (100)	39.5 (40)
Mustard	16 (7)	17 (9)	40 (41)	13 (5)	64 (81)	24 (17)	80 (97)	34 (32)
Ryegrass	–	–	47 (53)	16 (8)	63 (79)	24 (16)	88 (100)	41 (42.5)
Bare soil	–	–	29.5 (24)	9 (3)	53 (64)	20 (11)	73 (91)	24 (17)
SED (df)	–	–	4 (5)	–	4 (5)	2 (5)	–	4.5 (5)
P	ns	ns	0.04	ns	0.04[c]	0.01[c]	ns	0.08
Soil tillage								
Till	13 (5)	14 (5.5)	38 (37.5)	12.5 (5)	56 (69)	21 (13)	85 (99)	40 (42)
No-till	17 (8.5)	16 (8)	46 (51)	14.5 (6)	67 (85)	27 (21)	81 (98)	27 (21)
SED (df)	–	–	–	–	1 (1)	–	–	–
P	ns	ns	ns	ns	0.06[c]	ns	ns	ns
Fungicide								
Fungicide +	–	–	–	–	51 (60)	17 (8)	81 (98)	26 (20)
Fungicide−	–	–	–	–	72 (91)	31.5 (27)	89 (100)	55 (67)
SED (df)	–	–	–	–	1 (2)	1 (2)	–	–
P	–	–	–	–	0.002	0.005	ns	ns

Mean and level of significance (*P*-values and SED). ns, not significant; –, not determined; SED, standard error of difference; df, degrees of freedom.

[a]Data are arcsine transform values with, in brackets, the corresponding percentage values obtained by back transformation.

[b]Only main effects tested for LR203 because no plants were assessed in untreated wheat plots with summer fallow canopy followed by conventional tillage. Tests of significance for soil tillage and fungicide treatment effects correspond to unequal numbers of observations.

[c]Significant summer fallow crop and soil tillage interaction at $P = 0.05$.

Table 6. Take-all disease on nodal roots after the various summer fallow canopies relative to disease after wheat volunteers, in GS 33 at LR202. Mean differences[a] (summer fallow canopy − wheat volunteers) were tested and estimated by means of contrasts separately in tilled and no-tilled soil, for plots treated (F+) with silthiofam and untreated plots (F−)

Summer fallow canopy	Till				No-till			
	F+		F−		F+		F−	
	Incidence[b]	Severity[c]	Incidence[b]	Severity[c]	Incidence[b]	Severity[c]	Incidence[b]	Severity[c]
Oats	−28** (−22)	−9* (−3)	−40*** (−42)	−27*** (−20)	3 (0)	1 (0)	4 (0)	3 (0)
Oilseed rape	−12 (−4)	−4 (−0.5)	0 (0)	−7 (−1)	1 (0)	1 (0)	−6 (−1)	−2 (0)
Mustard	−16 (−8)	−6 (−11)	−22* (−14)	−20*** (−12)	6 (1)	2 (0)	7 (1.5)	3.5 (0)
Ryegrass	−3.5 (0)	−1 (0)	−24* (−16)	−20*** (−12)	1 (0)	−0.5 (0)	−3 (0)	0 (0)
Bare soil	−25* (−17)	−9* (−2)	−35** (−32)	−24.5*** (−17)	−1 (0)	0 (0)	−9 (2)	−5 (0)

*, **, *** – Fisher's test significant for $P = 0.05$, 0.01 and 0.001; GS 33 – mid-stem elongation (Zadoks et al., 1974); F−/F+ – untreated/treated plots.

[a]Data are arcsine transform values with, in brackets, the corresponding percentage values obtained by back transformation.

[b]SED (standard error of difference) for comparison between wheat volunteers and other summer fallow canopy treatment = 9.54 (10 df).

[c]SED (standard error of difference) for comparison between wheat volunteers and other summer fallow canopy treatment = 4.07 (10 df).

tween summer fallow crops and wheat volunteers only after tillage, for the oats, mustard, ryegrass and bare soil treatments. The summer fallow crops significantly decreased disease levels, by 22% to 42% for incidence and by 12% to 20% for severity (Table 6). Oats and bare soil decreased disease incidence to the greatest extent over the results obtained with wheat volunteers, whatever the fungicide treatment. Oilseed rape had no effect on disease incidence. Significant decreases in disease severity were observed only for untreated plots at this growth stage of wheat. The smallest difference in disease severity was obtained with oilseed rape. In the no-till plots, the mean differences in take-all levels between plots after wheat volunteers and after all other summer fallow crops were small, with no significant differences detected. All the effects described above were observed at the previous sampling time (GS 30); they persisted at GS 65 for disease severity but were no longer observed once disease had reached 100%.

In LR203, the epidemic was so strong and disease incidence so high that we were unable to detect the effects of the various treatments on disease incidence. A small summer fallow crop effect ($P = 0.08$) on severity was observed, with bare soil treatment resulting in the lowest disease severity, followed by mustard and oats. Thus, although ryegrass showed some potential to reduce disease levels from those obtained with the wheat volunteers treatment for LR202, this was not the case for the equivalent treatment in 2003, this crop giving results similar to those obtained with oilseed rape and wheat volunteers. In LR203, we were unable to test interactions between the main factors because of the lack of disease assessment in the untreated no-till plots due to the premature death of plants. Fungicide gave efficient protection but no significant effect. Lower severities were observed on treated plots.

Trial Gri201 showed no significant effect of summer fallow crops or soil tillage on take-all incidence at GS 32–33. Contrast analysis (table not shown) indicated that mustard followed by direct drilling significantly ($P < 0.05$) reduced the incidence, by 3% with respect to the wheat volunteers treatment. In contrast, mustard showed no significant difference with wheat volunteers treatment when followed by conventional tillage.

In long monoculture trials, the summer fallow crop had a significant effect on disease incidence (nodal roots) at GS 32–33 in Gri702 ($P = 0.04$) (Table 5), but no interaction with soil tillage was detected. In Gri601, mean disease incidence was higher after mustard than after wheat volunteers, whatever the soil tillage practice used. In Gri702, the highest mean disease incidence was obtained after wheat volunteers and the lowest, after bare soil. The difference between these two treatments was significant ($P < 0.05$) but no significant difference was observed between the other summer fallow crops, according to Student–Newman–Keuls test classification. The experimental factors had no effect on disease severity (Table 5) at GS 33. By the end of the cropping season, disease severity was significantly lower on the tilled plots than on the untilled plots.

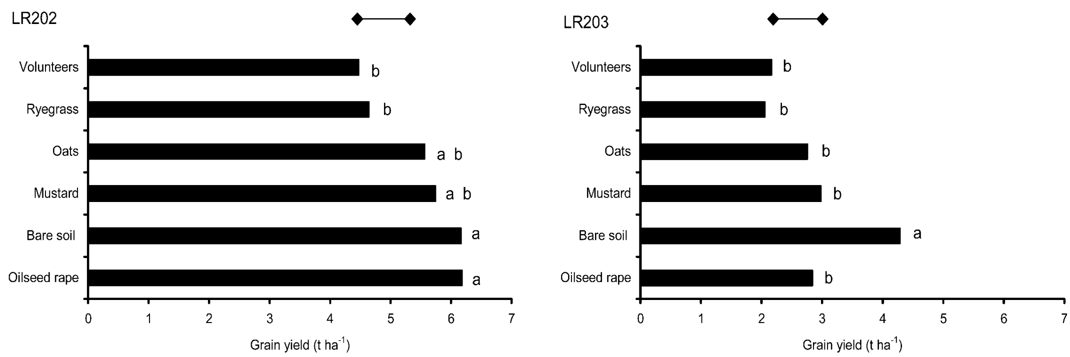

Figure 2. Grain yield (t ha^{-1}) at 16% water content, for Le Rheu trials. Horizontal bars represent the critical difference between two means (9.59 for LR202 and 7.93 for LR203). Bars followed by a common letter do not differ significantly according to analysis of variance and Student–Newman–Keuls test ($P = 0.05$).

Effects of summer fallow crops and soil tillage on yield

For yield, we observed no first- or second-order significant interactions between the three main factors. Yield was significantly increased by seed treatment in the Le Rheu trials ($P = 0.01$). Probably due to severe epidemics, this increase in yield resulted from both an increase in grain number per m^2 and 1000-grain weight. Summer fallow crop effects on yield were significant ($P < 0.05$) only at Le Rheu (Figure 2). Summer fallow crop effects on grain number per m^2 account for yield variations ($P = 0.01$). The highest mean yields were obtained after bare soil and oilseed rape (for LR202), and the lowest, after wheat volunteers and ryegrass ($P = 0.05$), whatever the soil tillage treatment. There was no significant difference with the remaining summer fallow crops (oats and mustard) (according to Student–Newman–Keuls classification). The effect of soil tillage was not significant, but mean yields obtained with the conventional tillage were higher than yields obtained with direct drilling.

In the Grignon 2001 trials, take-all caused negligible yield losses. The only significant effects on yield and its components were observed for Gri201, and concerned soil tillage. Direct drilling increased yield by increasing both grain number per m^2 and 1000-grain weight ($P = 0.05$).

Discussion

Differences in take-all epidemics between years and sites

The low severities observed at Grignon (Gri702), under long-term monocultures suggest that take-all decline had occurred. The relatively low mean severity values for all treatments indicate that an antagonistic microflora had developed during wheat monoculture (Cook, 1981). This microflora limited the extension of lesions (Sarniguet et al., 1992a). We observed differences in the magnitude of take-all decline. The decrease in disease observed in the 2001 cropping season (Gri601) was followed by more severe take-all the following year (Gri702), perhaps due to a weakening of take-all decline. Summer fallow crop had a significant effect on disease only at stage GS 32–33 in Gri702. This suggests that introducing summer fallow crops did not alter or break take-all decline in our experiments whereas such changes in take-all decline do occur following a break crop after a wheat monoculture (Lucas et al., 1989) and have been suggested in other studies of summer crops (Rothrock and Cunfer, 1986). At Le Rheu, we studied wheat crops preceded by only one year of wheat. Epidemics developed early, spread rapidly and very high levels of take-all were observed throughout the cropping season, in both experimental years. The Le Rheu experimental site is located in a region of maritime climate, well known to be conducive to take-all (Colbach et al., 1997; Schoeny and Lucas, 1999). It may also be more conducive than the Grignon experimental site. The following subsections focus mostly on Le Rheu.

Soil tillage effect

When summer fallow crops had an effect (significant difference from wheat volunteers treatment), this effect was generally greater or only detectable following soil tillage. Our results support the arguments developed by Moore and Cook (1984) in favour of conventional tillage for the management of the disease. In addition to providing a good seedbed and better control of weeds and volunteers, soil tillage increases contact between soil organic matter and crop residues. This contact activates microbial populations, and increases carbon mineralisation (Guérif, 1991), thus contributing to the rapid decay of residues harbouring the pathogen (Bockus et al., 1994; Bockus and Shroyer, 1998). In studies on no-tillage cropping systems, Wong and Southwell (1987) and Cook et al. (2002) observed an increase in the incidence of Ggt and *R. solani* (Rovira, 1986). Our results confirm these observations. In contrast, Brooks and Dawson (1968) and Rothrock (1987) claimed that no-tillage systems should reduce take-all infections. They suggested that tillage spread the fungus more widely on new nodal roots whereas, in no-tillage systems, large crop residues remain on the surface, while the seed is below, safe from contamination as Ggt may migrate by only 10 cm per year in undisturbed soil (Prew, 1980). Although the absence of tillage may delay the start of infection, significant spread on the nodal roots and progress on the stem base are observed because of immediate contact with infected residues.

Effects of summer fallow crop and interactions with soil-tillage treatment

It is well known that there are host and non-host crops of Ggt. In our field experiments, we focused on the effects of short-duration cropping in relationship to soil tillage practice. We did not try to analyse interactions between the soil micro-organisms responsible for these effects and the emission of allelopathic substances and their activity. We studied only the interaction between two types of residue: inoculum-infected residues from the previous crop and residues from summer fallow crops.

Wheat volunteer versus *bare soil plots*

Maintaining wheat volunteers between two successive wheat crops results in a high risk of take-all for the following wheat crop. The disease was best controlled by maintaining bare soil. Our results are consistent with those of Bockus et al. (1994), who showed that wheat volunteers can support fungal activity. They recommended eliminating volunteers. Host volunteer species (Cook, 2003), and weeds (Coventry et al., 1989) should be eliminated early so as to maximise the benefits. Roget et al. (1987) suggested applying herbicide to spontaneous volunteers, 3–6 weeks before sowing the next crop. This method worked well with another wheat pathogen, *R. solani*, for which damage to the subsequent wheat crop was significantly reduced with a direct-drilling system. In our experiments, some summer fallow crops were destroyed 2 weeks before the sowing of winter wheat, but others were destroyed only one day before sowing, which may be too late. The use of other dates might have led to levels of take-all intermediate between those observed with wheat volunteers and bare soil. It should also be noted that this strategy of summer fallow cleaning has an adverse effect on the environment due to deep drainage, nitrogen leaching and soil erosion.

Oilseed rape and mustard

Although oilseed rape is reputed to catch nitrogen, to protect the soil surface from erosion and to control soil-borne pathogens (Gardner et al., 1996; Buntin et al., 2002), it had no significant effect in our experiments. According to Kirkegaard et al. (1997), the efficiency of oilseed rape decreases with decreasing disease pressure, but disease pressure was high in all our trials. Despite the incorporation of residues after destruction, a whole cropping season with oilseed rape may be required to obtain the desired effect. Wheat crops grown after mustard suffered early attacks on seminal roots. These attacks may have stimulated antagonistic microbes restricting the extension of necrosis on the roots at late stages. Take-all levels were lower after mustard than after oilseed rape (Angus et al., 1994; Kirkegaard et al., 1994). However, in other contexts, mustard may be susceptible to other fungi, such as *R. solani* (Cook et al., 2002). The smallest numbers of wheat volunteers were observed with the mustard and oilseed rape treatments in Gri702. This may be due to competition for light between wheat and mustard or oilseed rape. This may contribute to the establishment and growth of the crop during the summer and hence to the success of summer fallow management. Seasonal conditions during summer fallow also influence both the growth of the summer fallow crop and the survival of the fungus. Summer rainfall events for example result in prolific growth of summer crops, while the fungus is preserved with dry conditions during this period (Kirkegaard et al., 2000) showing thereafter greatest benefits of the brassicas. Some studies have shown that the potential of the Brassicaceae for repressing pathogens depends on the type of soil (Bending and Lincoln, 1999) and the type of residue. Angus et al. (1994) observed that dried and irradiated roots of *Brassica* spp. significantly decreased Ggt growth but that young living roots had no significant effect. Kirkegaard and Sarwar (1999) observed that the isothiocyanate content of brassicas varied greatly among species and cultivars. In the field, the potential for disease suppression is variable; it is determined by climatic and inoculum preservation conditions (Kirkegaard et al., 2000). Further investigations with several cultivars are required to determine whether other cultivars would be more efficient.

Oats and ryegrass

In LR202, the best candidates for reducing take-all risk appeared to be oats, mustard and, surprisingly, to a lesser extent, ryegrass. These summer fallow crops decreased the disease only in association with conventional tillage. If Ggt inhibitors and avenacin (Turner, 1960; Osbourn et al., 1994) or biocidal components are secreted from oats and mustard, respectively, then conventional tillage may lead to these compounds being more widely distributed throughout the young root profile, resulting in greater contact with the infected residues. Alternatively, conventional tillage may have reduced the risk of disease by burying the infected residues. In France, Ggt is the most widespread variety of this fungus, with *Gaeumannomyces graminis* var. *avenae* (Gga) less common. Both are pathogenic on wheat and barley. However, in the long term, oats could support Gga, causing a shift in *G. graminis* populations from Ggt to Gga. The effects of ryegrass on take-all were particularly variable in our experiments. Ryegrass is known to behave in an ambiguous manner in terms of its effects on take-all. It may serve as a host of the fungus (Wehrle and Ogilvie, 1955; Slope and Etheridge, 1971; Coventry et al., 1989). It may also have an amplifying effect in the presence of a strong inoculum pressure (in association with hosts) (Colbach et al., 1994). However, in the absence of cereals, ryegrass behaves as a non-host crop. In this study, ryegrass may have stimulated the microflora antagonistic to Ggt (Wehrle and Ogilvie, 1955), including *Phialophora radicicola* (Slope et al., 1979) a fungus closely related to *G. graminis* var. *graminis*.

Fungicide effect

We did not focus on the effect of fungicide. Silthiofam has been shown to be effective in previous studies (Schoeny and Lucas, 1999), and seed treatment with this fungicide is already a widespread method of take-all control in France. Significant effects of summer fallow crops were observed in both plots treated with silthiofam and in untreated plots. Summer fallow crops tended to have a major effect at early stages in untreated plots (not shown) and at late stages in silthiofam-treated plots (at GS 65 for disease severity).

Yields

The lower yields observed with seeds not treated with silthiofam are consistent with results obtained by Schoeny et al. (2001). It should be noted that the observed yield differences between summer fallow crop treatments may have resulted from factors other than disease effect, such as soil mineral nitrogen, soil water content or soil structure. These factors may account for the higher yields observed after oilseed rape, which were not consistent with our disease assessments.

Our results show that summer fallow crops can help to reduce take-all levels in subsequent winter wheat crops. The effects of summer fallow crops cannot be accounted for solely by the non-host status of the plants grown. The way the summer fallow crop is managed before wheat sowing seems to be very important. Also, these effects have been established in a limited geographical range on two soil types in different years and weather conditions. It is important to mention that this alternative of introducing summer fallow crops into the cereal rotations to reduce take-all risk applies to sites where summer rainfall is not limiting, thereby permitting crops to grow enough and the expected effects be obtained. Further investigation is required to elucidate the effects of the plants on microbial changes and/or allelopathic effects. The interaction between the infectious residues of the previous wheat crop and the residues of the summer fallow crop is also not fully understood. We found that leaving the soil bare during the summer strongly reduced disease incidence and severity. The economic feasibility of this strategy has yet to be demonstrated: the appropriate trade-off between the cost-effective use of summer fallow, the limitation of take-all epidemic risks and the consequences for yield losses requires further work.

Acknowledgements

We are grateful to J.-F Fourbet and O. David for advice and assistance with statistical analysis of data, and A. Schoeny for advice, and M. Gosme for supplying some of the data for the Le Rheu 2003 trial. We thank S. Carrillo, B. Le Fouillen and C. Bouchard for technical assistance, and J. Troizier and S. Carrillo for conducting our field trials. We also thank J. Sappa for linguistic improvement, and the senior editor and the reviewers for helpful comments and suggestions on the manuscript. This work was financed by INRA, ARVALIS and Monsanto Europe S. A.

References

Angus JF, Gardner PA, Kirkegaard JA and Desmarchelier JM (1994) Biofumigation: Isothiocyanates released from Brassica roots inhibit growth of the take-all fungus. Plant and Soil 162: 107–112

Bending GD and Lincoln SD (1999) Characterisation of volatile sulphur-containing compounds produced during decomposition of *Brassica juncea* tissues in soil. Soil Biology and Biochemistry 31: 695–703

Bockus WW and Shroyer JP (1998) The impact of reduced tillage on soilborne plant pathogens. Annual Review of Phytopathology 36: 485–500

Bockus WW, Davis MA and Norman BL (1994) Effect of soil shading by surface residues during summer fallow on take-all of winter wheat. Plant Disease 78: 50–54

Brisbane PG and Rovira AD (1988) Mechanisms of inhibition of *Gaeumannomyces graminis* var. *tritici* by fluorescent pseudomonas. Plant Pathology 37: 104–111

Brooks DH and Dawson MG (1968) Influence of direct-drilling of winter wheat on incidence of take-all and eyespot. Annals of Applied Biology 61: 57–64

Brown PD and Morra MJ (1995) Glucosinolate-containing plant tissues as bioherbicides. Journal of Agriculture and Food Chemistry. 43: 3070–3074

Brown PD and Morra MJ (1997) Control of soil-borne plant pests using glucosinolate-containing plants. Advances in Agronomy 61: 167–231

Bullock DG (1992) Crop rotation. Critical Reviews in Plant Sciences 11: 309–326

Buntin GD, Raymer PL, Bednarz CW, Phillips DV and Baird RE (2002) Winter crop, tillage, and planting date effects on double-crop cotton. Agronomy Journal 94: 273–280

Colbach N (1995) Modélisation de l'influence des systèmes de culture sur les maladies du pied et des racines du blé tendre d'hiver, Thèse, Institut National Agronomique Paris-Grignon

Colbach N and Meynard JM (1995) Soil tillage and eyespot: influence of crop residue distribution on disease development and infection cycles. European Journal of Plant Pathology 101: 601–611

Colbach N, Lucas P and Cavelier A (1994) Influence des successions culturales sur les maladies du pied et des racines du blé d'hiver. Agronomie 14: 525–540

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

Cook RJ (1981) The influence of rotation crops on take-all decline phenomenon. Phytopathology 71: 189–192

Cook RJ (1994) Problems and progress in the biological control of wheat take-all. Plant Pathology 43: 429–437

Cook RJ (2003) Review. Take-all of wheat. Physiological and Molecular Plant Pathology 62: 73–86

Cook RJ, Schillinger WF and Christensen NW (2002) Rhizoctonia root rot and take-all of wheat in diverse direct-seed spring cropping systems. Canadian Journal of Plant Pathology 24: 349–358

Cotterill PJ and Sivasithamparam K (1988) Inoculum of the take-all fungus in rotations of wheat and pasture: relationships to disease and yield of wheat. Transactions of the British Mycological Society 91: 63–72

Coventry DR, Brooke HD, Kollmorgen JF and Ballinger DJ (1989) Increases in wheat yield on limed soil after reduction of take-all by fungicide application and crop rotation. Australian Journal of Experimental Agriculture 29: 85–89

Doran JW (1980) Soil microbial and biochemical changes associated with reduced tillage. Soil Science Society of American Journal 44: 765–771

Dulout A, Lucas P, Sarniguet A and Doré T (1997) Effects of wheat volunteers and blackgrass in set-aside following winter wheat crop on soil infectivity and soil conduciveness to take-all. Plant and Soil 197: 149–155

Gardner PA, Pitson GD and Angus JF (1996) Control of take-all of wheat with chloride, break crops, fungicide, fumigation and micro-organisms. In: 8th Australian Agronomy Conference. The Regional Institute, Toowoomba

Guérif J (1991) Influence de la simplification du travail du sol sur l'état structural des horizons de surface: conséquences sur leurs propriétés physiques et leurs comportements mécaniques. In: INRA (ed.) Les Colloques. Vol. 65. Paris (pp. 13–33)

Hornby D, Bateman GL, Gutteridge RJ, Lucas P, Osbourn AE, Ward E and Yarham DJ (1998) Take-all Disease of Cereals. A Regional Perspective, CAB International, Wallingford, UK

Kirkegaard JA and Sarwar M (1999) Glucosinolates profiles of Australian canola (*Brassica napus annua* L.) and Indian mustard (*Brassica juncea* L.) cultivars: implications for biofumigation. Australian Journal of Agriculture Research 50: 315–324

Kirkegaard JA, Gardner PA, Angus JF and Koetz E (1994) Effect of Brassica break crops on the growth and yield of wheat. Australian Journal of Agriculture Research 45: 529–545

Kirkegaard JA, Hocking PJ, Angus JF, Howe GN and Gardner PA (1997) Comparison of canola, Indian mustard and linola in two contrasting environments. II. Break-crops and nitrogen effects on subsequent wheat crops. Field Crops Research 52: 179–191

Kirkegaard JA, Sarwar M, Wong PTW, Mead A, Howe G and Newell M (2000) Field studies on the biofumigation of take-all by *Brassica* break crops. Australian Journal of Agriculture Research 51: 445–456

Kollmorgen JF and Walsgott DN (1983) Saprophytic survival of *Gaeumannomyces graminis* var. *tritici* at various depths in soil. Transactions of the British Mycological Society 82: 346–348

Lemaire JM and Coppenet M (1968) Influence de la succession céréalière sur les fluctuations de la gravité du piétin-échaudage (*Ophiobolus graminis* Sacc.). Annales des Epiphyties 19: 589–599

Lockwood JL (1986) Soilborne plant pathogens: concepts and connections. Phytopathology 76: 20–27

Lucas P, Sarniguet A, Collet JM and Lucas M (1989) Réceptivité des sols au piétin échaudage (*Gaeumannomyces graminis* var. *tritici*): influence de certaines techniques culturales. Soil Biology and Biochemistry 21: 1073–1078

Mazzola M, Granatstein DM, Elfving DC and Mullinix K (2001) Suppression of specific apple root pathogens by

Brassica napus seed meal amendment regardless of glucosinolate content. Phytopathology 91: 673–679

McEwen J, Darby RJ, Hewitt MV and Yeoman DP (1989) Effects of field beans, fallow, lupins, oats, oilseed rape, peas, ryegrass, sunflowers and wheat on nitrogen residues in the soil and on the growth of a subsequent wheat crop. Journal of Agriculture Science, Cambridge 115: 209–219

Moore KJ and Cook RJ (1984) Increased take-all of wheat with direct drilling in the Pacific Northwest. Phytopathology 74: 1044–1049

Osbourn AE, Clarke BR, Lunness P, Scott PR and Daniels MJ (1994) An oat species lacking avenacin is susceptible to infection by *Gaeumannomyces graminis* var. *tritici*. Physiological and Molecular Plant Pathology 45: 457–467

Picard D, Saulas P and Ghiloufi M (2000) Contribution to the development of cropping systems with permanent cover and which avoid plough-layer inversion. In: Third International Crop Science Congress, Hamburg (pp 17–22)

Potter MJ, Davies K and Rathjen AJ (1998) Suppressive impact of glucosinolates in *Brassica* vegetative tissues on root lesion nematode *Pratylenchus neglectus*. Journal of Chemical Ecology 24: 67–80

Prew RD (1980) Studies on the spread of *Gaeumannomyces graminis* var. *tritici* in wheat. I. Autonomous spread. Annals of Applied Biology 94: 391–396

Prew RD and Dyke GV (1979) Experiments comparing 'break crops' as a preparation for winter wheat followed by spring barley. Journal of Agricultural Science, Cambridge 92: 189–201

Roget DK, Venn NR and Rovira AD (1987) Reduction of Rhizoctonia root rot of direct-drilled wheat by short-term chemical fallow. Australian Journal of Experimental Agriculture 27: 425–430

Rothrock CS (1987) Take-all of wheat as affected by tillage and wheat–soybean doublecropping. Soil Biology and Biochemistry 19: 307–311

Rothrock CS and Cunfer BM (1986) Absence of take-all decline in double-cropped fields. Soil Biology and Biochemistry 18: 113–114

Rothrock CS and Langdale GW (1989) Influence of nonhost summer crops on take-all in double-cropped winter wheat. Plant Disease 73: 130–132

Rovira AD (1986) Influence of crop rotation and tillage on rhizoctonia bare patch of wheat. Phytopathology 76: 669–673

Sarniguet A, Lucas P and Lucas M (1992a) Relationships between take-all, soil conduciveness to the disease, populations of fluorescent pseudomonads and nitrogen fertilizers. Plant and Soil 145: 17–27

Sarniguet A, Lucas P, Lucas M and Samson R (1992b) Soil conduciveness to take-all of wheat: influence of the nitrogen fertilizers on the structure of populations of fluorescent pseudomonads. Plant and Soil 145: 29–36

SAS Institute (1989) SAS/STAT User's Guide. Version 6, SAS Institute, Cary, NC

Schoeny A and Lucas P (1999) Modeling of take-all epidemics to evaluate the efficacy of a new seed-treatment fungicide on wheat. Phytopathology 89: 954–961

Schoeny A, Jeuffroy M-H and Lucas P (2001) Influence of take-all epidemics on winter wheat yield formation and yield loss. Phytopathology 91: 694–701

Simon A and Sivasithamparam K (1988) Crop rotation and biological suppression of *Gaeumannomyces graminis* var. *tritici* in soil. Transactions of the British Mycological Society 91: 279–286

Slope DB and Etheridge J (1971) Grain yield and incidence of take-all (*Ophiobolus graminis* Sacc.) in wheat grown in different crop sequences. Annals of Applied Biology 67: 13–22

Slope DB, Prew RD, Gutteridge RJ and Etheridge J (1979) Take-all, *Gaeumannomyces graminis* var. *tritici*, and the yield of wheat grown after ley and arable rotations in relation to the occurrence of *Phialophora radicicola* var. *graminicola*. Journal of Agricultural Science, Cambridge, 93: 377–389

Turner EMC (1960) The nature of the resistance of oats to the take-all fungus. III. Distribution of the inhibitor in oat seedlings. Journal of Experimental Botany 11: 403–412

Wehrle VM and Ogilvie L (1955) Effect of ley grasses on the carry-over of take-all. Plant Pathology 4: 111–113

Weller DM and Cook RJ (1983) Suppression of take-all of wheat by seed treatment with fluorescent pseudomonads. Phytopathology 73: 463–469

Werker AR, Gilligan CA and Hornby D (1991) Analysis of disease–progress curves for take-all in consecutive crops of winter wheat. Plant Pathology 40: 8–24

Wong PTW (1975) Cross-protection against the wheat and oat take-all fungi by *Gaeumannomyces graminis* var. *graminis*. Soil Biology and Biochemistry 7: 189–194

Wong PTW and Southwell RJ (1987) Saprophytic survival of the take-all fungus and its antagonist, *Gaeumannomyces graminis* var. *graminis* under conventional and no-tillage. Soil and Tillage Research 9: 355–362

Zadoks JC, Chang TT and Konzak CF (1974) A decimal code for the growth stages of cereals. Weed Research 14: 415–421