

Next WGIN Stakeholder meeting – 22 November 2011, RRes, Harpenden

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Defra Wheat Genetic Improvement Network – Improving the environmental footprint of farming through crop genetics and targeted traits analysis

Background

The UK government is committed to more sustainable agriculture but this vision is facing an ever expanding range of environmental, energy and climate change challenges. Wheat is grown on a larger area and is more valuable than any other arable crop in the UK. Established in 2003, the Wheat Genetic Improvement Network (WGIN) arose directly from a realisation in the early 2000s that over the preceding two decades there had widening disconnection been а between commercial plant breeding activities and publicly funded plant and crop research. The overall aim of WGIN is to generate pre-breeding material carrying novel traits for the UK breeding companies and to deliver accessible technologies, thereby ensuring the means are available to produce new, improved varieties. An integrated scientific 'core' which combines underpinning work on molecular markers, genetic and genomic research, together with novel trait identification, are being pursued to achieve this goal. The programme is managed by a team including representatives of the key UK research groups and breeders. They ensure the programme and its outputs are communicated to the wider scientific and end user communities, via a web site, a stakeholder forum, focused meetings and peer reviewed publications. WGIN liaises with equivalent operations overseas to ensure the programme is internationally competitive.

The initial WGIN project ran for five years (2003-2008) and achieved considerable scientific success. In addition, the sustained networking activities and the availability of datasets generated by the project led to the establishment of many new wheat genetic improvement projects, including some funded jointly by the public sector and industry. Those funded by early 2008 were summarised in the May 2008 Stakeholders Newsletter and since then several additional projects have been agreed. There is no doubt that WGIN has a direct and significant impact on relationship re-establishing the between commercial plant breeding activities and public funded plant and crop research. However significant hurdles remain which currently prevent commercial implementation of much new research which should help to reduce the energy requirement and environmental impact of the UK wheat crop.

This project

The new WGIN Core Project started in 2008 to provide genetic and molecular resources for research in other defra projects and for a wide range of wheat research projects in the UK. The resources under development include wheat genetic stocks, mapping populations, molecular marker markers and technologies, trait identification and evaluation, genomics and bioinformatics. The initially funded partners are the John Innes Centre, Rothamsted Research and The University of Nottingham but support has been allocated for sub-contracted projects which were awarded in open competition during 2009.

Objective 2: Near Isogenic Lines (JIC)

Bringing precision to marker assisted selection for UK wheat breeding

WGIN has developed the Avalon x Cadenza mapping population as a reference for UK wheat genetics research and breeding. However, the discovery of genes segregating in this population is much more meaningful when compared to the segregation of the same genes in different crosses grown in multiple environments that reflect the increasing variability that new varieties are exposed to. Through a process called QTL meta analysis the WGIN team at JIC have collated information for multiple traits, in multiple environments, in multiple segregating populations. The output from this analysis for one gene on wheat chromosome 3A is shown below in **Figure 1**. This gene influences multiple aspects of development in bread wheat, in this case represented as flowering time.



Figure 1 ' Quantitative Trait Loci (QTL) located on wheat chromosome 3A which control flowering time. These QTL are superimposed on one genetic map although they were identified in multiple populations (Avalon x Cadenza, Spark x Rialto, Charger x Badger, and Savannah x Rialto) and multiple environments.

After showing that genes like this are common in UK wheat varieties and stably expressed in diverse growing situations the WGIN team set about genetic and physiological dissection of gene function by developing precise genetic stocks referred to as Near Isogenic Lines (NILs). Figure 2 shows a set of lines designed to vary, as much as possible, only for the 3A target gene. In the first instance this approach validates the meta QTL but more importantly it allows us to the transition make from the studying gene as а entity statistical within а population to a simple genetic locus. This means we can map the location of the gene to a very high resolution, going on to



identify the precise DNA difference that causes the difference in crop characteristics between varieties with and without the gene. For the physiologist and agronomist these precise genetic stocks allow detailed experiments, not possible on larger populations, which define the interactions of a gene with the environment. Together this approach allows very precise breeding of new varieties with defined complements of genes to maximise performance with minimal agronomic inputs. The WGIN project is developing an extensive set of NILs for stature, development, grain yield, bread making quality, and efficient use of fertiliser. Objective 7 Insect resistance in wheat: Cereal aphids

Assessing the differential susceptibility to two cereal aphid species of targeted lines from the Spark x Rialto mapping population

The major cereal aphid pests of UK wheat, the grain aphid, *Sitobion avenae*, and the bird-cherry oat aphid, *Rhopalosiphum padi*, are both vectors for Barley Yellow Dwarf Virus (BYDV). Although they can be controlled by insecticides, the development of insect resistant wheat varieties would provide growers with a sustainable alternative to broad spectrum toxicants. In previous work, (reported in the October 2009 Newsletter) 17 lines from the mapping population,

at 24h. These data were then compared for statistically significant differences and the number of nymphs produced was expressed as a proportion of the nymphs produced on Solstice in the same assay, thus providing a "preference index" for both aphid species. The most and least preferred lines were not the same for *R. padi* and *S. avenae*. However, there were a few lines where the responses coincided and one in particular, SR120 was very susceptible to both aphids (Figure 3).



produced from the crossing of UK varieties Spark and Rialto, were tested against *R. padi* and *S. avenae* in laboratory bioassays. Replicated groups of 10 alate (winged) aphids were given the choice between two seedlings, one of a standard variety, Solstice and the other of the test variety. The number of alates settled and the number of nymphs produced on each seedling was recorded There were no obvious differences between the leaf surfaces of SR120, the two parental lines and Solstice when examined under UV high powered stereo microscope, which ruled out that particular aspect of leaf morphology from affecting aphid settlement. More detailed developmental assays were performed for eight of the lines from the mapping population, chosen from the most and least preferred lines for each aphid species, plus the two parental lines and

Solstice. Fifteen replicated groups of 5 or 6 alates were placed in clip cages, attached to leaves of test wheat seedlings and left overnight to produce nymphs. Neonate nymphs, collected the following morning, were weighed in batches of 5 in a 0.2ml Eppendorf tube on a microbalance and then transferred to the first leaf of 7-8 day old seedlings of Solstice, as the standard variety, or of the test line. At least 12 batches of nymphs were set up on each plant line and each batch was enclosed in a clip cage (Figure 4).



Figure 4 Clip cage enclosing aphid nymphs

Surviving nymphs were re-weighed in their batches after 7 days and the Mean Relative Growth Rate (MRGR) was calculated as: MRGR = (In 7day weight – In birth weight) / number of days (7)



All data were subjected to ANOVA to determine any significant differences. The MRGR of the aphids on each line is presented as a proportion of the MRGR on Solstice in the same trial (Figure 5).

There were no significant differences between MRGR on the lines compared to Solstice for either aphid except for R. padi on line SR67. Excepting line SR67. settlement preference of alates did not relate to the development rate of the nymphs. These data are now being checked to

determine whether there is any genetic basis to the effects with the possibility of creating a new mapping population between SR120 and SR67.

Objective 8: Update on nitrogen use efficiency component

The eighth WGIN variety/N-trial was completed in 2011. In addition to assessing performance and variation in a variety of sub-traits contributing to yield and nitrogen use efficiency (NUE), this multiyear trial is enabling trait stability to be assessed in a diverse set of seasons.

2011 also suffered a very dry spring, negatively impacting on tillering. Late rain again ensured some yield recovery but also resulted in the occurrence of immature grain in the final harvest. Yield data and quality (N) have yet to be analyzed.



Figure 6 - Aerial photograph of Meadow field at Rothamsted in 2011 (19th May). The main trial is the WGIN Diversity Trial, which is designed with 3 replicate blocks, each of which is subdivided into 4 N regimes. There are 25 varieties and each plot has a protected yield area and a smaller area for destructive sampling. In the top left of the field, the Wheat Prebreeding LOLA Diversity Trial can be seen.

Summarising the 2010 season (7th WGIN variety/N trial), the dry pre-flowering period resulted in low tillering and low yields, resulting in a compression of both genotypic and N-treatment variation. The consequent rain during grain filling ensured efficient N-uptake with consequent high grain N and protein, however delays to harvesting caused by continuing rain resulted in disappointing final quality (low HFN).

population was grown in the field with 200 kg/ha N fertilizer. The trial was phenotyped for post anthesis canopy longevity as well as for the basic set of NUE parameters (grain/straw yields/N contents). Another trial will be planted this autumn for 2012 harvest, and will be supplied with 100 kg/ha N. The population is also being phenotyped for root traits in greenhouse based experiments.

in 2011 were Crusoe and Stigg, chosen for their potential canopy longevity characteristics and for 2012 Conqueror, Hereford and Zeberdee. The 2012 new varieties have been chosen to overlap the NUE studies with WGIN work both on WUE and take-all.

New varieties

The Avalon x Cadenza double haploid mapping

Objective 9: Improvement of water use efficiency and drought tolerance traits.

Wheat is the most extensive arable crop in the UK. It is increasingly affected by drought. New varieties may be one way of combating these drought effects. However, breeders may need to look for different characteristics and change the way they assess new candidates if genetic effects are to be exploited. The physiological basis of

improved drought tolerance amongst varieties 18 has been analysed in a field experiment at University of Nottingham in 2010/11 to guide breeding future strategies to improve drought tolerance. Researchers at Nottingham have examined associations between grain yield under drought and a range of physiological screens for drought

Figure 7 - Measurement of canopy green area using the Crop Scan spectroradiometer in WGIN drought tolerance experiment at Sutton Bonington in June 2011

performance including leaf water-use efficiency assessed by carbon isotope discrimination (Δ^{13} C) of flag leaf and grain samples; leaf transpiration assessed by oxygen isotope discrimination (Δ ¹⁸O) of leaf samples; leaf photosynthesis (Psi chlorophyll fluorpen, Licor 6400 photosynthesis system), leaf senescence (Cropscan spetroradiometer) and accumulation of stem soluble carbohydrate reserves shortly after flowering. One of the most interesting findings coming out of this work is the possible value of grain $\Delta^{13}C$ as an indicator drought of performance.

This trait appears to be positively correlated with grain yield under drought, and during 2010/11 a field experiment at Nottingham has characterised grain Δ^{13} C in 94 lines of a doubled-haploid population derived from a cross between Rialto x Savannah. All the field experiments in 2010/11 (18 cultivar panel and 94 DH lines of Rialto x

Savannah DH population under irrigated and unirrigated conditions at UoN and 94 DH lines of Rialto x Savannah DH population under unirrigated conditions at John Innes Centre) experienced significant drought stress in unirrigated treatments providing a good test-bed for the analysis of drought-tolerance

traits in WGIN. Genetic analysis is ongoing to identify quantitative trait loci

(QTL) associated with grain Δ^{13} C and other drought-tolerance traits that can be used to develop molecular markers to screen for drought tolerance in plant breeding programmes. Field experiments to test the Rialto x Savannah DH population in a second season have been successfully established at both Nottingham and JIC in September/October 2012. The research team carrying out the work comprises John Foulkes and Jayalath De Silva at UoN and Simon Griffiths and Simon Orford at JIC.

Objective 10: Take-All disease (RRes)

Resistance to take-all in the diploid wheat Triticum monococcum

Take-all, caused by the fungus *Gaeumannomyces graminis* var *tritici*, is one of the most damaging diseases of wheat and barley in the UK and elsewhere. This primarily soil-borne fungus attacks cereal roots. In severely infected fields the disease, which often occurs in patches, causes stunted plants, premature senescence, white heads and a severe loss of yield. This disease is

most prevalent in short rotations and when consecutive wheat crops are in the 2nd and 3rd rotation positions. Global research over the past thirty years has failed to identify any good sources of resistance in hexaploid wheat germplasm.

T. monococcum is a diploid $\dot{A}^{m}A^{m}$ wheat (2n=2x=14)genome), also referred to as einkorn wheat, which is closely related to the hexaploid wheat. Although domesticated 8000 years ago and dominating early human farming activity, Τ. monococcum has been infrequently used in wheat breeding. Wheat genetic improvement often relies on the enlargement of gene pools by introducing novel traits from closely-related germplasm.

In WGIN1, we started to screen the Rothamsted collection of Research Т. monococcum accessions for resistance to the Take-all fungus. In both field and controlled environment experiments, large variation in the development of Take-all disease symptoms was found amongst Τ. monococcum accessions. Some T. the monococcum accessions exhibited a similar level of susceptibility to take-all as hexaploid wheat varieties. In contrast, other T. monococcum accessions had much low levels of root disease. These results were first reported in the autumn 2007 WGIN Stakeholders Newsletter.

Since 2008 we have evaluated the most promising *T. monococcum* accessions on a yearly basis using either 5 or 10 replicated plots per genotype. In these trials we have included, to serve as the benchmark controls, several other cereal species, namely hexaploid wheat (highly susceptible), triticale (moderately resistant), rye (highly resistant) and oats (not infected).

Three years of field data are now available for the *T. monococcum* – Take-all resistance screen, i.e. for the harvest years 2008, 2010 and 2011. In 2009 only a limited number of accessions were screened (data not shown). Each trial was done as a 3rd wheat crop. In these three field trial years the disease pressures were very different:



2008 was a particularly severe take-all year, 2010 a moderate disease year and 2011 a slight disease year (Figure 8). A Take-all Index scoring system was used to quantify both disease incidence and disease severity (Bateman GL, Gutteridge RJ, Jenkyn JF, (2004) Annals of Applied Biology 145, 317-330). Two Τ. monococcum accessions (MDR046 and MDR031) were found to restrict Take-all root infection to levels that were intermediate to those observed on triticale and rye roots. This occurred in all three Some other accessions seasons. dave promisingly low disease scores, for example MDR286. In addition, these trials have confirmed that some other T. monococcum accessions are as susceptible to Take-all disease as the fully susceptible hexaploid wheat cultivar Hereward. In trial years 2009 and 2011, very low SED values were obtained. We now as standard use 10 replicated plots to evaluate each accession.



Legends for Figures 8, 9 and 10

Assessment of Take-all disease symptoms in various accessions of the diploid wheat *T. monococcum*. Several cereal species were included to serve as benchmark controls. Shown are results from three years of field trials. The take-all index definition and calculation was adopted from a previous study (Bateman GL, Gutteridge RJ, Jenkyn JF, 2004, Annals of Applied Biology 145, 317-330). In field harvest years 2010 and 2011, all genotypes were assessed using 5 replicated plots / line.

Based on these field results the most promising resistance lines have been crossed to the intermediately susceptible accession MDR37 and the generation of several mapping populations is in progress via single seed descent. The genetic basis of Take-all resistance will be explored in the future using the F_6 generation and screening in pot tests and field trials.

PUBLICATIONS

McMillan, V., Hammond-Kosack, K. E., Kanyuka, K. and Gutteridge, R. (2011). A new approach to reduce the risk of Take-all disease. Rothamsted Research Association (RRA) Newsletter, April 2011, 2 pages (available as a pdf from the WGIN website).

Burt C, Nicholson P. JIC (2011). Exploiting co-linearity among grass species to map the *Aegilops ventricosa*- derived *Pch1* eyespot resistance in wheat and establish its relationship to *Pch2*. Theoretical and Applied Genetics. In Press

Andrew J. Macdonald & Richard J. Gutteridge. Effects of take-all (*Gaeumannomyces graminis* var. *tritici*) on crop N uptake and residual mineral N in soil at harvest of winter wheat. Plant & Soil. Accepted October 2011.

IMPACT ON OTHER RESEARCH

WGIN is now into its eighth year. To assess its impact on other research, members of the UK science and wheat breeding community were approached over the last couple of months to give feedback on their use of WGIN data, tools and resources.

The tables on the following pages contain information we have received so far on new projects that have used WGIN data in their grant proposal applications.

Table 1: Projects using WGIN data in grant proposal applications									
Principal Investigator	Co-PIs	PI location	General Research Topic	Sponsor	Project type	Project Title	Duration: from to	Funding amount (total) in £	WGIN Inputs
Sarah Holdgate (RAGT)	Kim Hammond-Kosack, Richard Gutteridge, Peter Jack, Peter Werner, Simon Berry	Rothamsted Research, RAGT Seeds Ltd, KWS UK Ltd and Limagrain UK Ltd	Low take-all inoculum build up	BBSRC,TSB	Technology Strategy Board: New approaches to Crop Protection	Protecting second wheat through the reduction of take-all inoculum build up	2010 - 2015	£247,000	1, 3
Andy Phillips (RRes)	Alison Huttly, Simon Vaughan	Rothamsted Research	Pre-harvest sprouting in white wheat	BBSRC	Responsive mode	Investigating the role of flavonoid biosynthesis in coat-imposed dormancy to facilitate the breeding of white-grained varieties of wheat.	2010 - 2013	£602,358	1, 4
Andy Phillips (RRes)	Cristobal Uauy	Rothamsted; Research, John Innes Centre	TILLING in wheat	BBSRC	BBR	Provision of tilling resources and platforms in wheat	2011 - 2012	£220,302	4
Andy Phillips (RRes)	none	Rothamsted Research	Novel height alleles	Lawes Trust	PhD	Interaction between dwarfing genes and the environment in the control of wheat stature.	2009 - 2013	£70,000	4
Andy Phillips (RRes)	Steve Thomas	John Innes Centre	Novel height alleles	Rothamsted International	Visiting scholar	The application of TILLING as a reverse genetic approach for gene function and breeding in durum wheat	2011 - 2012	£18,000	4
C Uauy (JIC)	V Foster, P. Werner, S. Berry, P. Jack, T Henrisksson	John Innes Centre	Preharvest Sprouting, QTL, fine mapping	Defra, BBSRC, HGCA and industry consortium	LINK	A 'breeder's tool kit' to improve Hagberg Falling Number for the economic and environmental sustainability of UK wheat	2010 - 2014	£1,340,020	1
Neil Paveley (ADAS)	John Foulkes, James Brown and Luis Mur	Uof Nottingham, John Innes Centre, and U of Aberystwyth	Costs of disease resistance	Defra, BBSRC, HGCA and industry consortium	SA-LINK	Screening for 'costs of disease resistance' caused by stomatal dysfunction.	2010 - 2014	£443,761	1

Table 1 Continued									
Graham Moore (JIC)	JIC: Simon Griffiths, RRes: Peter Shewry, Malcolm Hawkesford, John Pickett, Kim Hammond-Kosack, Univ Nottingham: Ian King , John Foulkes, Univ Bristol: Keith Edwards, Gary Barker; NIAB Andy Greenland	John Innes Centre, Rothamsted Research, University of Bristol, University of Nottingham, NIAB	Wheat pre-breeding	BBSRC	LoLa	Enhancing diversity in UK wheat breeding through a public sector prebreeding programme	2011 - 2014	£7,000,000	3, 5, 6, 8, 9
Peter Shewry	Malcolm Hawkesford	Rothamsted	Grain quality, plant			Improving the N response	2008 -		
(RRes)	(RRes)	Research	nutrition	BBSRC, HGCA	BBSRC IPA	of UK wheat varieties	2012	£639,399	10, 11
Peter Shewry (RRes)	Paola Tosi	RRes/Campden BRI	Grain quality	BBSRC, Campden BRI	Industrial CASE PhD studentship	Spatial patterns of protein deposition in wheat Genetic improvement of	2008 - 2012	£75,000	10, 11
Nigel Halford (RRes)	Simon Griffiths and others	RRes, John Innes Centre	Genetic control of asparagine accumulation in wheat grain	BBSRC and industry consortium	LINK	wheat to reduce the potential for acrylamide formation during processing	2011 - 2015	£936,000	1, 6
Simon Griffiths (JIC)	many EU based PIs	John Innes Centre	Breeding tools	EU Framework 7	EU	ADAPTAWHEAT-Genetics and physiology of wheat development to flowering: tools to breed for improved adaptation and yield potential		£500,000	2
Pete Berry (ADAS)	Simon Griffiths	ADAS, JIC, Limagrain and BASF	Resource Use Efficiency	Defra, BBSRC, HGCA and industry consortium	LINK	Exploiting novel genes to improve resource use efficiency in wheat		£274,477	2, 6
Keith Edwards (U of Bristol)	Simon Griffiths	Bristol University	Genotyping platform	BBSRC		Development and validation of a flexible genotyping platform for wheat		£217,000	1, 2, 5, 12
Hannah Jones (U of Reading)	Simon Griffiths	University of Reading	Heat stress at anthesis	BBSRC	Responsive mode	Genetic diversity and yield stability for increased resilience against climate change in the UK		£537,185	2

Table 1: Continued.									
Steve Hoad (SAC)	David Laurie, Luzie Wingen	SAC, Edinburgh, John Innes Centre	Wheat ear sterility	Scottish Government (RESAS), HGCA, BBSRC and industry consortium	DEFRA LINK	Control of infertility in wheat by phenotype screening and genetic analysis of varieties and breeding lines. Wheat Ear Sterility Project (WESP)	2009 - 2013	£341,270	1
Donal O'Sullivan (NIAB)	Rosemary Bayles (NIAB), Simon Griffiths (JIC)	NIAB, Huntingdon Road	Yellow rust resistance genes	John Oldacre Foundation	PhD	"Study of the genetic basis of specific and partial resistance to rust diseases in UK wheat cultivars using association analysis"	2009 - 2011	£45,000	1
Donal O'Sullivan (NIAB)	Rosemary Bayles (NIAB), James Brown (JIC)	NIAB, Huntingdon Road	Multiple disease resistance to foliar pathogens	BBSRC	LINK	Wheat Association Genetics for Trait Advancement and the Improvement of Lineages	2011 - 2015	£478,233	1, 9
Steven Bentley (NIAB)	Andy Greenland, Emma Wallington	NIAB	Grain Quality	DEFRA,HGCA	SA-LINK	Evaluation of low phytate wheat	2005 - 2009	£755,937	13
Andy Greenland (NIAB)	Nick Gosman, Phil Howell, Dave Laurie	NIAB/JIC	Pre-breeding	BBSRC, HGCA and Industry consortium	BBSRC CSI/IPA	Pre-breeding at NIAB; synthetic wheats and flowering time	2005 - 2012 TOTAL	£649,760 £15.390.702	3

Footnotes:

- 1 Avalon x Cadenza DH mapping population and marker information
- 2 Avalon x Cadenza NILs
- 3 Phenotyping methods
- 4 Cadenza EMS population
- 5 AE Watkins collection
- 6 Gediflux collection
- 7 TILLING technology
- 8 Triticum monococcum accessions
- 9 Other JIC mapping populations
- 10 NUE diversity trial
- 11 Grain samples from WGIN field trials
- 12 Chinese Spring x Paragon mapping population
- 13 Paragon EMS population

TSB - Technology Strategy Board and part sponsored by Industry LINK- Project part sponsored by industry

The University of Nottingham

Forthcoming events:

WGIN Stakeholders Meeting 22 November 2011, RRes Programme Wheat Genetic Improvement Network

10:00 Arrival and coffee

- 10:15 Welcome Peter Shewry, RRes
- 10:20 Wheat Market Update Helen Plant, AHDB

The Wheat Genetic Improvement Network

- 10:40 WGIN: Overview and update on RRes WGIN research *Kim Hammond-Kosack, RRes*
- 11:00 Avalon x Cadenza gene discovery for UK farming Simon Griffiths, JIC
- 11:20 Dissecting nitrogen use efficiency Malcolm Hawkesford, RRes
- 11:40 Coffee

End user developments

- 12:00 Update on Global Wheat Genebanks and Information Systems Mike Ambrose, JIC
- 12:20 Adapting wheat to global warming Roger Sylvester Bradley, ADAS
- 12:40 An update on GM wheat field trials Huw Jones, RRes
- 13:00 Lunch with posters on wheat research

Wheat initiatives

- 14:00 The Crop Improvement Club Progress so far Jayne Brookman, BBSRC
- 14:20 Update on Wheat Genome Sequencing Initiative Graham Moore, JIC
- 14:40 Update on Sustainable Agriculture and Food Innovation Platform– *Calum Murray, TSB*
- 15:00 Bio break

Successful 2nd and 3rd Wheat Crops

15:30 Introduction to Discussion panel on "Successful 2nd and 3rd Wheat Crops" and issue of Take-all – *Kim Hammond-Kosack, RRes*

Discussion Chair: Peter Shewry, RRes

Panellists:

- Mark Dodds, Wheat Breeder, KWS
- David Knott, Farms Manager, Trumpington Farming Company, Cambs
- Andrew Richards, Crop Agronomist, Masstock
- Phil Humphrey, Crop Agronomist, The Arable Group
- Kerry Maguire Cereal Pathologist, NIAB
- Ian Clark Soil Microbiologist, RRes
- Pete Berry Principal Research Scientist, ADAS
- Adrian Peck Farmer, Cambs and HGCA board member
- Steve McGrath Soil Expert, RRes
- 17:10 Tea and finish

For further information on the WGIN project please see www.wgin.org.uk or contact us at

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The contributors to this newsletter were: At Rothamsted Research: Kim Hammond-Kosack, Malcolm Hawkesford, Lesley Smart, and Suzanne Thrussell. At the John Innes Centre: Simon Griffith, Luzie Wingen, and Simon Orford. At the University of Nottingham: John Foulkes and Jayalath De Silva.

