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The effect of agronomic factors on crop health and performance of winter wheat varieties bred for the conventional and the low input farming sector

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ABSTRACT

It has been frequently suggested that varieties bred/selected under conventional farming conditions lack important traits required for optimum performance under low agrochemical input conditions. However, there is limited scientific information about interactions between cultivars bred/selected for the low input vs conventional farming sector and innovative crop agronomic strategies on crop health, yield and quality parameters to support this hypothesis. The main objective of this pilot study was therefore to compare the effect of contrasting fertilisation and crop protection regimes used in organic and conventional farming on crop health and performance parameter in two wheat varieties developed for organic/low input and conventional farming systems respectively.

Results indicate that both leaf phenolic and flavonoid compounds, were positively associated with use of the ‘long straw’ variety Aszita and to a lesser extent composted FYM fertiliser inputs, while they were negatively associated with mineral N-fertiliser inputs, plant N uptake and use of the ‘short straw’ variety Solstice. On the other hand foliar and ear disease severity were positively associated with plant N uptake, use of the variety Solstice and the use of mineral fertilisers, while they were negatively associated with composted FYM fertiliser inputs, leaf phenolic/flavonoid concentrations and the use of the variety Aszita.

Overall findings suggest that low input farming-focused breeding programmes might deliver varieties such as Aszita that have lower yield potential, but have higher grain protein, leaf phenolic concentrations, and foliar disease resistance under low-input conditions. Future studies should investigate whether the higher foliar phenolic levels found in low input varieties are linked to disease resistance and if they are also expressed in the grain.

1. Introduction

The demand for organic food has increased rapidly over the last 25 years in many developed countries in Europe, North America, and Asia/Oceania (Willer and Kilcher, 2011). Demand is mainly driven by consumer perceptions that organic farming is more sustainable, and

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delivers environmental, biodiversity, animal welfare, and food quality and safety benefits compared to intensive conventional farming (Joshi and Rahman, 2015; Stolz et al., 2011).

Organic farming standards, which are defined by government laws and regulations in most countries (EC, 2017; USDA, 2017; Willer and Kilcher, 2016, 2017), prohibit or restrict the use of many external inputs that are widely used in conventional farming, primarily because they are non-renewable, scarce (e.g. mineral P, K and micronutrient fertilisers) and/or energy intensive to produce (e.g. mineral N fertilisers) and are potentially deleterious to the environment and human health (e.g. mineral N and P fertilisers, synthetic chemical pesticides, antibiotics, food additives). Specifically, organic crop production standards prohibit the use of synthetic chemical crop protection products (fungicides, herbicides, insecticides, plant growth regulators) and the main mineral fertilisers (all sources of N, KCl and superphosphate) that are used widely in conventional farming systems (Baker et al., 2002; EC, 2017; USDA, 2017). Instead, organic crop production standards prescribe regular inputs of organic fertilisers (e.g. manure and composts), use of legume crops in the rotation (to increase N-levels and balance N:P ratios in the soil) and application of preventative and non-chemical crop protection methods (e.g. the use of more diverse crop rotations, more resistant/tolerant varieties, mechanical weeding, and biological disease and pest control products). However, organic standards permit the use of certain plant or microbial extracts and/or minerals (e.g. Cu and S) for crop protection (EC, 2017; Hansen 2010, USDA, 2017). As a result, organic and conventional crop production protocols differ substantially in the type and quantities of fertilisers applied, crop protection methods, and increasingly also in the types of varieties used (Bilsborrow et al., 2013; Lehesranta et al., 2007).

It has been frequently suggested that varieties (and especially cereal cultivars) developed for and selected under conventional farming conditions lack important traits/trait combinations required for optimum performance under organic/low-input conditions and that there is a need to develop crop varieties that are more suitable for organic and other low input farming systems (Lammerts van Bueren et al., 2010; Wolfe et al., 2008). As a result, organic/low-input breeding programmes have been established for some crops (including cereals) by breeders in both Europe and the USA where their main selection criteria are based on resistance or tolerance to biotic and abiotic stresses, high resource-use efficiency as well as high end-use quality and adaptation to local microclimates (Crespo-Herrera and Ortiz, 2015). For winter wheat such programmes are often based on crosses between modern high yielding, short straw varieties and older land-races with longer straw, with subsequent selection of progeny in an organic production environment (Murphy et al., 2007).

Phenolic acids and flavonoids are the main types of antioxidants found in cereal grains and their consumption has been linked to a reduction in certain chronic diseases in humans (Del Rio et al., 2013). Also, in cereals and other crop plants the activation of the phenylpropanoid pathway is thought to be an important component of resistance against foliar diseases such as powdery mildew and *Fusarium* (Bollina et al., 2010; Sander and Heitefuss, 1998; Siranidou et al., 2002). However, to our knowledge the metabolic responses of cereals to necrotrophic pathogens such as *Septoria tritici* are not well documented. In winter wheat, foliar phenolic concentrations and resistance against powdery mildew were shown to decrease with increasing mineral N-fertiliser inputs (Sander and Heitefuss, 1998), while recent studies have shown that the contrasting fertilisation and crop protection practices used in organic and conventional systems result in substantial differences in secondary metabolite profiles, crop health, nutritional composition and gene and protein expression patterns (Arncken et al., 2012; Baker et al., 2002; Barański et al., 2014; Cooper et al., 2011; Lammerts van Bueren and Myers, 2012; Lehesranta et al., 2007; Rempelos et al., 2018, 2013; Shepherd et al., 2014; Tetard-Jones et al., 2013; van Dijk et al., 2009). There is also virtually no information on the performance (particularly crop health, yield and quality parameters) of different varieties bred/ selected for the organic vs the conventional farming sector grown using organic and conventional farming practices (e.g. crop rotation designs, fertilisation and crop protection)

The main objectives of this 2 year pilot study were to carry out factorial field experiments to: (i) compare the performance of two winter wheat varieties, developed via conventional (Solstice) and organic/low-input (Aszita) farming focused breeding/selection programmes under contrasting fertilisation and crop protection protocols; (ii) identify interactions between variety choice, fertilisation regime, crop protection protocols with respect to leaf phenolic/flavonoid compound concentrations and their relationship with resistance against certain foliar fungal diseases in organic and conventional wheat production systems; and (iii) assess the relative importance of genetic and agronomic (fertilisation and crop protection) factors/ drivers for phenolic profiles, and crop health and performance parameters using redundancy analyses.

2. Materials and methods

2.1. Site description

The variety plots of the Nafferton Factorial Systems Comparison (NFSC) trials were originally set up in 2009 on a field with a uniform sandy loam at Nafferton Experimental Farm (Newcastle University) to provide a facility for in depth study of the effect of fertility type, crop protection and genotype on yield, resource use efficiency as well as gene, protein and metabolite expression of cereal and potato crops under the EU-funded NUE CROPS project.

2.2. Field experimental design

The experiment has a split-split-split plot factorial design with (1) fertility type (main plot; 24 × 24 m), (2) fertility level (sub-plot; 24 × 24 m), (3) crop protection (sub-sub-plot; 12 × 24 m) and (4) variety choice sub-sub-sub-plot; 1.5 × 24 m) as factors and 4 replicate blocks. This design allows the experiment to be analysed as a 2 × 2 × 2 × 2 factorial experiment with fertility type (composted FYM vs mineral N-fertiliser inputs), fertility level (170 and 85 kg total N ha^{-1}), crop protection (with and without use of synthetic fungicides, herbicides and growth regulators), and variety choice (Aszita: long straw variety bred for organic systems; Solstice: typical short straw variety bred for conventional systems) as factors.

2.3. Agronomic protocols and crop assessments

The winter wheat varieties Aszita (Sativa Seeds Ltd.) and Solstice (Horizon Seeds Ltd.) were sown in late October of 2009 and 2011 using a commercial drill (3 m Lely combination drill; Lely UK Ltd, St Neots, UK). Seed used in conventional crop protection plots were produced using standard commercial seed production protocols which included insecticide and fungicide seed treatments. Seed used in organic crop protection plots were produced according to organic seed production standards (Soil Association, Bristol, UK) and were untreated. Details of the fertilisation (including the NPK composition of manure) and crop protection protocols (products used, application timings and rates), soil NPK content and the climatic conditions in the two different growing seasons are provided in the supporting information (Table S1 and Figure S1).

Septoria Leaf Blotch (*Septoria tritici*), Yellow (Stripe) Rust (*Puccinia striiformis*) and Powdery mildew (*Blumeria. graminis* f. sp. tritici) disease severity (% infected leaf area) was assessed weekly on both the flag leaf (L1) and leaf 2 (L2) from the start of spring growth as described in Bilsborrow et al.(2013). Powdery mildew severity was almost zero in both seasons and data are therefore not presented. Leaning/ lodging severity was also assessed and the% area of a plot showing leaning/ lodging was recorded. Leaning/lodging was defined as cereal tillers/

stems bending over at an angle of ≥45° or laying on the ground. The severity of stem based diseases, which are a contributing factor to leaning/lodging, was not recorded.

Crops from all plots/treatment combinations were harvested using a plot combine harvester (Claas Dominator 38; Claas UK Ltd, Bury St Edmunds, UK) and grain samples were dried (hot air drying using an electric motor fed through a 3 m × 1.5 m × 0.70 m wooden box with a meshed surface for grain sacks to rest on) and cleaned using a Lainchbury HC1/7 W grain cleaner (Blair Engineering, Blairgowrie, UK) immediately after harvest. Biomass production and total N uptake by the crop was determined at anthesis (GS63) and at crop maturity by harvesting all above-ground biomass from 4 randomly selected 0.5 m long rows in each plot. All samples were dried (70 °C) immediately to prevent translocation of N from storage organs to the grain. Plant samples taken at GS63 were separated into ears, leaves and stems. The harvest index (HI) was calculated as the ratio between grain yield and above-ground biomass, while the Nitrogen Harvest Index (NHI) was calculated as the ratio between grain N and above-ground biomass N. Total N uptake for each growth stage was calculated by multiplying the plant biomass (kg ha^{-1}) by the plant N concentration (g N kg^{-1}). Wheat flag leaves were sampled in each plot at the start of flowering (GS63) according to Zadoks et al. (1974).

2.4. Analysis of leaf macro-micro nutrient, phenolic acid and flavonoid concentrations

Approximately 100–200 flag leaves from each plot were collected and immediately frozen, lyophilised, and milled as described in Tetard-Jones et al. (2013). All plant material was analysed for total N by Dumas combustion (Elementar Vario Macro Cube (Elementar, DE). Other macro-, micro- nutrients in flag leaves and grain were determined by subjecting leaves to acid digestion (HNO_3) in a closed-vessel microwave reaction system (MarsExpress; CEM Corp., Matthews, NC, USA) and analysis with an inductively coupled argon plasma optical emission spectrometer (ICP-OES) as described in Cooper et al. (2011). Soil mineral N in the top 30 cm of soil was measured at GS20 (~March each year); soil NO_3-N and NH_4-N concentrations were measured by extracting soil samples with 2 M KCl and analysis of extracts with a Seal auto analyser 3, as previously described by Orr et al. (2011).

A standard method was used for the extraction of phenolics from plant leaves as described by Bennett et al. (2003). Extracts were analysed by HPLC on a Shimadzu Prominence HPLC system equipped with an LC-20AD pump, SIL-20AC autosampler, and SPD-M20A photodiode array detector (Shimadzu Corp. Kyoto, Japan) according to Rempelos et al. (2018).

2.5. Statistical analysis

The effects of harvest year, fertility type, fertility level, crop protection and variety choice on wheat grain yield, disease severity and flag leaf phenolic content were assessed using ANOVA derived from a linear mixed-effects model (Pinheiro and Bates, 2000). The hierarchical nature of the split-split-plot designs was reflected in the random error structures that were specified as harvest year/block/fertility type/fertility level/crop protection. The normality of the residuals of all models was tested using QQ-plots. Differences between the four crop management strategies were tested using Tukey contrasts in the general linear hypothesis testing (glht) function of the multcomp package in R (Hothorn et al., 2008). A linear mixed effects model was used for the Tukey contrasts, containing a treatment main effect, with four levels, with the random error term specified as described above.

The relationships between wheat phenolic compounds, disease severity and agronomic factors, were investigated using partial redundancy analysis (pRDA) which summarises the part of functional trait composition' variation that is explained by selected environmental variables, after removing the effects of other variables (block = replicate) and by using the CANOCO 5 software (Ter Braak and Šmilauer, 2012). Automatic forward selection of the agronomic or phenolic factors within the RDAs was used and their significance in explaining additional variance calculated using Monte Carlo permutation tests. Spearman's rank-based correlation analysis were performed using the correlation testing (cor.test) function in R. Correlation matrixes were visualised with correlograms using the corrplot package in R (Friendly, 2002).

3. Results

Climatic conditions differed across the two experimental seasons (2009/2010 and 2011/2012), with substantially lower average temperatures and solar radiation, but higher rainfall levels in the 2011/2012 compared to the 2009/2010 growing season (March to August). On the other hand, average wind speeds in July and August (the period when lodging risk is greatest) were higher in 2010 than 2012 (Fig. S1).

3.1. Phenolic acid and flavonoid concentrations

Significant main effects of fertiliser input type, and variety were detected for concentrations of both total phenolic acids and flavonoids in the flag leaf. Concentrations of total phenolic acids and flavonoids were higher in composted FYM fertilised plants and when the variety Aszita was used. In addition, there were significant main effects of crop protection for total phenolic acid concentrations (which were higher with organic crop protection) and year for flavonoid concentrations (which were higher in the warm/dry year 2010 compared to the cool/wet 2012). There was also a trend ($P = 0.07$) towards significantly higher phenolic acid concentrations in 2010 compared to 2012 (Table 1). Main effect means and ANOVA P values for the effects of harvest year, fertility type, fertility input level, crop protection and variety choice on flag leaf phenolic acids and flavonoids are shown in Tables S2-S4.

There was a significant 2-way interaction between year and variety and a significant 3-way interaction between years, fertiliser input type and variety for both total phenolic acid and flavonoid concentrations (Table 1). When the 3-way interaction was further investigated, there were no significant differences in phenolic acid and flavonoid concentration between varieties in the cool/wet year 2012, while in the warm/dry year 2010 composted FYM fertilised plants of the variety Aszita had significantly higher phenolic acid and flavonoid concentrations than Solstice (Fig.1a, b). In contrast, when mineral fertiliser was used in 2010 Aszita had significantly higher concentrations of phenolic acids but the same levels of flavonoids compared to Solstice (Fig.1a, b)

3.2. Foliar disease severity and lodging

The only foliar diseases causing quantifiable amounts of symptoms on leaves were *Septoria tritici* and yellow rust (*Puccinia striformis*). In addition to foliar disease severity the proportion of the ears covered by fungal disease was also recorded prior to harvest but the fungal pathogens on ears were not identified (Table S5).

Significant main effects of fertility type (at L1 only) and variety (but not year, fertility input level or crop protection) were detected, with the use of composted FYM fertiliser and the variety Aszita resulting in lower levels of *Septoria* (Table 2). For the flag leaves (L1) significant 2-way interactions between (a) fertility input level and variety; (b) crop protection and variety (Table 2; Fig S4) and a significant 3-way interaction between fertility input type, crop protection and variety were detected (Table 2). For Leaf 2 (L2) significant 2-way interactions between (a) fertility input type and crop protection and (b) fertility input type and variety (Table 2; Fig. S4) and a significant 3-way interaction between fertility input type, fertility input level and variety were detected (Table 2; Fig. 2b).

Fig. 2a and b describes the nature of the 3-way interactions detected

Table 1
Effects of fertility type, fertility level, crop protection and genotype on total chlorogenic acid, total hydroxicinamic acid, total phenolic acid and total flavonoid concentration in wheat flag leaves.

means ± SE	Total chlorogenic acids mg g^{-1}	Total hydroxicinamic acids mg g^{-1}	Total phenolic acids mg g^{-1}	Total flavonoids mg g^{-1}
Harvest year				
2010 (*n* = 64)	12.8 ± 0.68	4.8 ± 0.19	17.7 ± 0.81	19.8 ± 0.74
2012 (*n* = 64)	7.9 ± 0.72	3 ± 0.25	10.9 ± 0.83	4.7 ± 0.4
Fertiliser type (FT)				
Compost (*n* = 64)	12.5 ± 0.84	4.1 ± 0.27	16.6 ± 1	13.8 ± 1.23
Mineral (*n* = 64)	8.2 ± 0.56	3.7 ± 0.23	11.9 ± 0.74	10.7 ± 0.96
Fertiliser input level (FL)				
170 kg N ha^{-1} (*n* = 64)	10.1 ± 0.77	4 ± 0.27	14.1 ± 0.94	11.9 ± 1.09
85 kg N ha^{-1} (*n* = 64)	10.7 ± 0.76	3.8 ± 0.23	14.5 ± 0.92	12.7 ± 1.15
Crop protection				
Conventional (*n* = 64)	9.4 ± 0.68	3.7 ± 0.23	13.1 ± 0.82	11.9 ± 1.12
Organic (*n* = 64)	11.3 ± 0.83	4.1 ± 0.27	15.4 ± 1	12.7 ± 1.12
Variety				
Aszita (*n* = 64)	11.4 ± 0.95	4.8 ± 0.27	16.2 ± 1.11	14.3 ± 1.31
Solstice (*n* = 64)	9.3 ± 0.5	3 ± 0.17	12.3 ± 0.6	10.2 ± 0.82
ANOVA				
Main effects				
Harvest year (YR)	*0.0827*	*0.0923*	*0.0711*	**0.0013**
Fertiliser type (FT)	**0.0033**	ns	**0.0033**	**0.0034**
Fertiliser input level (FL)	ns	ns	ns	ns
Crop protection (CP)	**0.0106**	*0.0661*	**0.0072**	ns
Variety (VR)	**0.0031**	**< .0001**	**< .0001**	**< .0001**
Interactions				
YR × FT	ns	ns	ns	**0.0335**
YR × FL	ns	ns	ns	ns
FT × FL	ns	**0.0336**	ns	ns
YR × CP	ns	ns	ns	ns
FT × CP	*0.0889*	ns	*0.0992*	ns
FL × CP	ns	ns	ns	ns
YR × VR	**0.0002**	ns	**0.0002**	< .0001
FT × VR	ns	*0.0617*	*0.0753*	**0.0155**
FL × VR	ns	ns	ns	ns
CP × VR	ns	ns	ns	ns
YR × FT × FL	ns	ns	ns	ns
YR × FT × CP	ns	ns	ns	ns
YR × FL × CP	ns	ns	ns	ns
FT × FL × CP	ns	ns	ns	ns
YR × FT × VR	**0.0011**	ns	**0.0036**[1]	**0.0026**[1]
YR × FL × VR	ns	*0.0961*	ns	ns
FT × FR × VR	ns	ns	ns	ns
YR × CP × VR	ns	ns	ns	ns
FT × CP × VR	ns	ns	ns	ns
FL × CP VR	ns	ns	ns	ns
YR × FT × FL × CP	ns	ns	ns	ns
YR × FT × FL × VR	ns	ns	ns	ns
YR × FT × CP × VR	ns	ns	ns	ns
YR × FL × CP × VR	ns	ns	ns	ns
FT × FL × CP × VR	ns	ns	ns	ns
YR × FT × FL × CP × VR	ns	ns	ns	ns

[1] See Fig. 1 for interactions means ± SE.

for *Septoria* severity on the flag leaf and leaf 2 respectively. When composted FYM was used as fertiliser there was no significant effect of using conventional crop protection inputs (fungicide, herbicides and growth regulators) on *Septoria* severity on flag leaves, and the relative differences in disease severity between Aszita and Solstice were similar (Fig. 2a). In contrast, when mineral N-fertiliser was used in combination with conventional crop protection, Septoria disease severity was significantly higher in Solstice than Aszita (Fig. 2a).

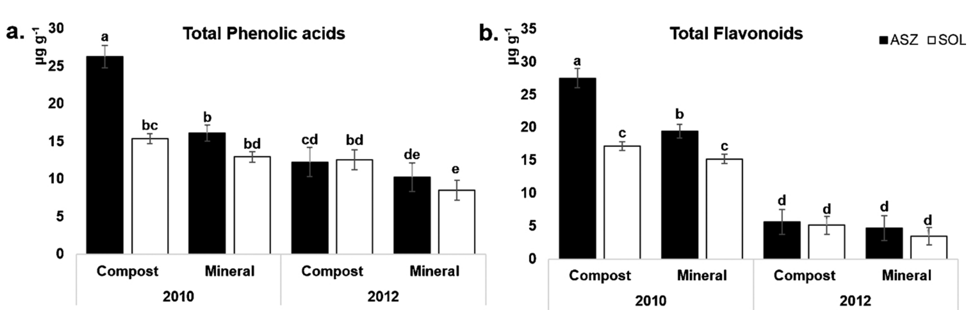

Fig. 1. Interactions (means ± SE) between year, fertility type and variety for flag leaf: (a) total phenolic acids and (b) total flavonoid concentration at GS63.

Table 2
Effects of fertility type, fertility level, crop protection and genotype on grain yield, harvest index, grain protein and leaf disease severity.

means ± SE	*Septoria tritici* Leaf 1 AUDPC	*Septoria tritici* Leaf 2 AUDPC	*Grain Yield t ha^{-1}	Harvest Index %	Grain Crude Protein %
Harvest year					
2010 (*n* = 64)	237.6 ± 17.76	273.7 ± 24.37	4 ± 0.23	44.8 ± 1.23	10.7 ± 0.22
2012 (*n* = 64)	205.9 ± 15.16	244.8 ± 21.54	3.1 ± 0.17	29.6 ± 1.16	10.9 ± 0.22
Fertiliser type (FT)					
Compost (*n* = 64)	186.6 ± 16.27	246.2 ± 23.35	2.9 ± 0.14	35.2 ± 1.19	10.1 ± 0.2
Mineral (*n* = 64)	256.9 ± 15.79	272.2 ± 22.66	4.2 ± 0.23	39.3 ± 1.77	11.4 ± 0.22
Fertiliser input level (FL)					
170 kg N ha^{-1} (*n* = 64)	217.5 ± 17.73	257.4 ± 23.45	3.8 ± 0.24	38 ± 1.55	11.1 ± 0.24
85 kg N ha^{-1} (*n* = 64)	226 ± 15.44	261.1 ± 22.68	3.3 ± 0.16	36.4 ± 1.5	10.4 ± 0.19
Crop protection					
Conventional (*n* = 64)	201.8 ± 14.27	252.2 ± 20.84	3.8 ± 0.22	38.6 ± 1.55	10.8 ± 0.21
Organic (*n* = 64)	241.7 ± 18.36	266.3 ± 25.07	3.3 ± 0.18	35.9 ± 1.49	10.8 ± 0.24
Variety					
Aszita (*n* = 64)	168 ± 13.16	193.4 ± 19.45	3.3 ± 0.16	34.5 ± 1.45	12 ± 0.19
Solstice (*n* = 64)	275.5 ± 16.98	325.1 ± 23.42	3.8 ± 0.24	40 ± 1.53	9.5 ± 0.12
ANOVA					
Main effects					
Harvest year (YR)	ns	ns	ns	**0.0114**	ns
Fertiliser type (FT)	**0.0347**	ns	**0.018**	**0.0455**	**0.0001**
Fertiliser input level (FL)	ns	ns	ns	ns	**0.0005**
Crop protection (CP)	ns	ns	**0.0007**	*0.0648*	ns
Variety (VR)	**< .0001**	**< .0001**	**< .0001**	**0.0002**	**< .0001**
Interactions					
YR × FT	ns	ns	**0.0127**[2]	ns	**0.0007**
YR × FL	ns	ns	ns	ns	ns
FT × FL	ns	ns	*0.0937*	ns	**0.0001**[3]
YR × CP	ns	ns	ns	ns	ns
FT × CP	ns	**0.0005**[5]	ns	ns	ns
FL × CP	ns	ns	ns	ns	ns
YR × VR	ns	ns	**< .0001**[2]	**0.0319**[1]	**< .0001**[3]
FT × VR	ns	**0.0041**[5]	**< .0001**[2]	ns	**0.004**[3]
FL × VR	**0.0035**[4]	ns	*0.0536*	ns	ns
CP × VR	**0.0378**[4]	ns	ns	ns	**0.0289**[3]
YR × FT × FL	ns	ns	ns	ns	ns
YR × FT × CP	ns	ns	ns	ns	ns
YR × FL × CP	ns	ns	ns	ns	ns
FT × FL × CP	ns	ns	ns	ns	*0.0998*
YR × FT × VR	ns	ns	**0.0183**[1]	ns	**< .0001**[3]
YR × FL × VR	ns	ns	ns	ns	ns
FT × FR × VR	*0.0522*	**0.0316**[1]	ns	ns	**0.0018**[3]
YR × CP × VR	ns	ns	*0.0978*	**0.005**[1]	ns
FT × CP × VR	**0.0079**[1]	ns	**0.0265**[1]	ns	*0.0661*
FL × CP VR	ns	ns	ns	ns	ns
YR × FT × FL × CP	ns	ns	ns	ns	ns
YR × FT × FL × VR	ns	ns	ns	ns	**< .0001**[1]
YR × FT × CP × VR	ns	ns	ns	ns	**0.0135**[1]
YR × FL × CP × VR	ns	ns	ns	ns	ns
FT × FL × CP × VR	ns	ns	ns	ns	ns
YR × FT × FL × CP × VR	ns	ns	ns	ns	ns

[1] See Fig. 2 for interactions means ± SE; [2] See Fig. S2 for interactions means ± SE; [3] See Fig. S3 for interactions means ± SE; [4] See Fig. S4 for interactions means ± SE; [5] See Fig. S5 for interactions means ± SE.
* Dry matter yield.

Septoria disease on leaf 2 was similar with all four fertiliser regimes (high and low composted FYM and mineral fertiliser inputs) for cultivar Aszita (Fig. 2b). In contrast, for the cultivar Solstice, mineral N-fertiliser resulted in a higher disease severity than was observed for composted FYM, but only under the higher fertiliser input level (Fig. 2b). Also, significant differences in *Septoria* disease severity between the two varieties were only detected when mineral N fertilisers were used (Fig. 2b). Figures describing the 2-way interactions detected for *Septoria* severity are in the supplementary information (Fig. S4).

Virtually no yellow rust symptoms were found on Aszita. In Solstice substantial yellow rust was only found in crops that were fertilised with mineral N fertilisers (on the flag leaf only when the high N input level was used) under organic crop protection (not treated with conventional fungicide/herbicide/growth regulator sprays). Detailed results on main effects, and interactions between, experimental factors are provided in the supplementary information (Table S5; Fig. S6).

Virtually no stem lodging was found in Solstice, which had significantly shorter stems. On the other hand stem lodging in Aszita was more severe in the dry/warm year 2010 (Table S5), which was also characterised by stronger winds (higher average wind speeds) than 2010 (Fig. S1). In the variety Aszita, lodging was most severe in mineral N fertilised crops under organic crop protection (not treated with conventional fungicide/herbicide/growth regulator sprays) in both years. Detailed results on main effects, and interactions between, experimental factors are provided in the supplementary information (Table S5; Fig. S5).

3.2.1. Drivers for foliar/ear disease severity and stem lodging

When associations between phenolic acids, agronomic protocol, variety choice drivers/explanatory variables, and disease severity were analysed by RDA the explanatory variables accounted for 41.6% of variation. Axis 1 explained 35.7% of the variation with axis 2 a further

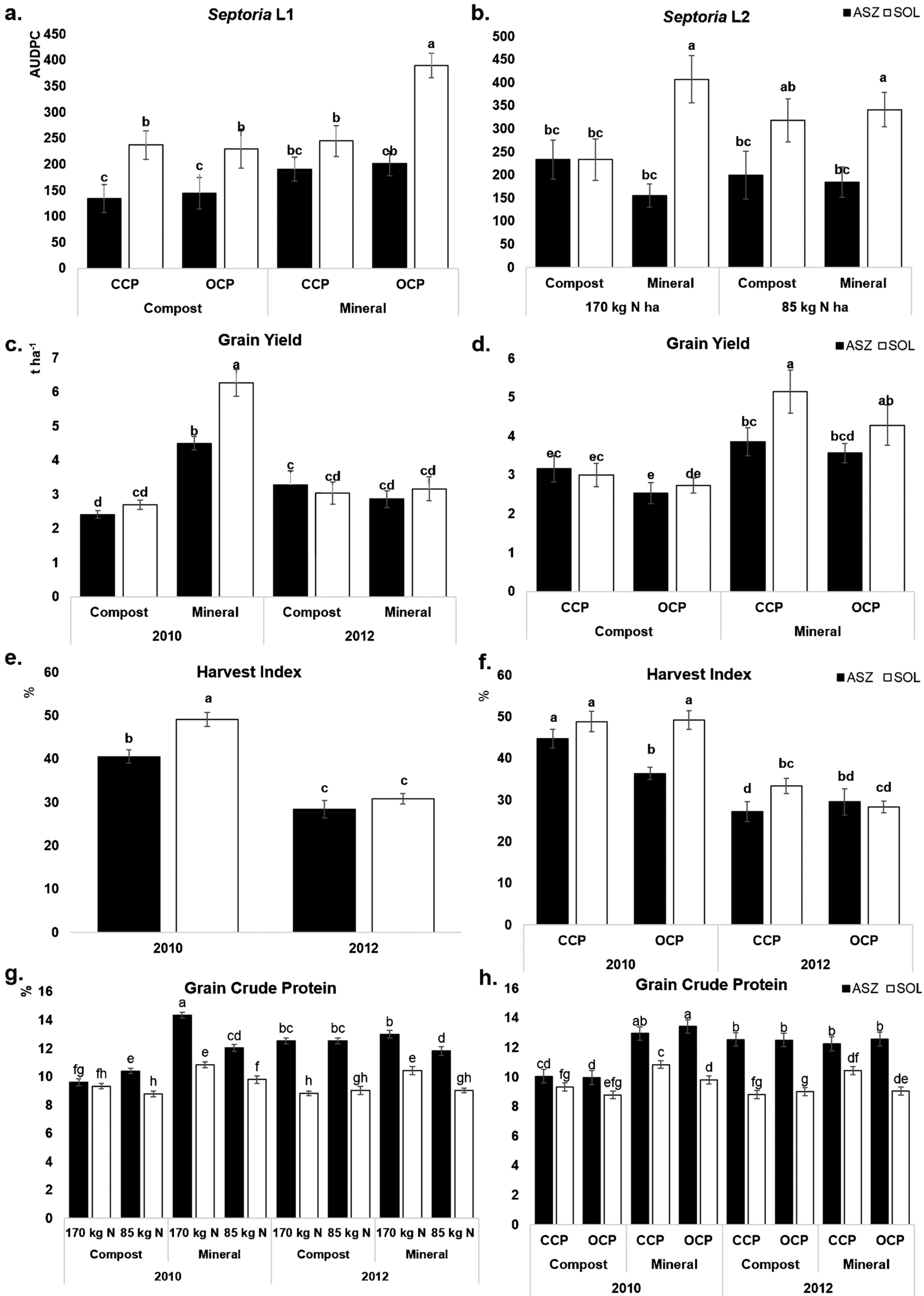

Fig. 2. Interactions (means ± SE) between (a) year, fertiliser type and variety; (b) fertiliser type, crop protection and variety for grain yield (DM); (c) fertiliser type, crop protection and variety for *Septoria* severity at flag leaf; (d) fertiliser input level, fertiliser type and variety for *Septoria* severity at leaf 2; (e) year and variety and (f) year, crop protection and variety for harvest index; (g) Year, fertiliser type, fertiliser input and variety and (h) year, fertiliser type, crop protection and variety for gran protein content; CCP: conventional crop protection; OCP: organic crop protection.

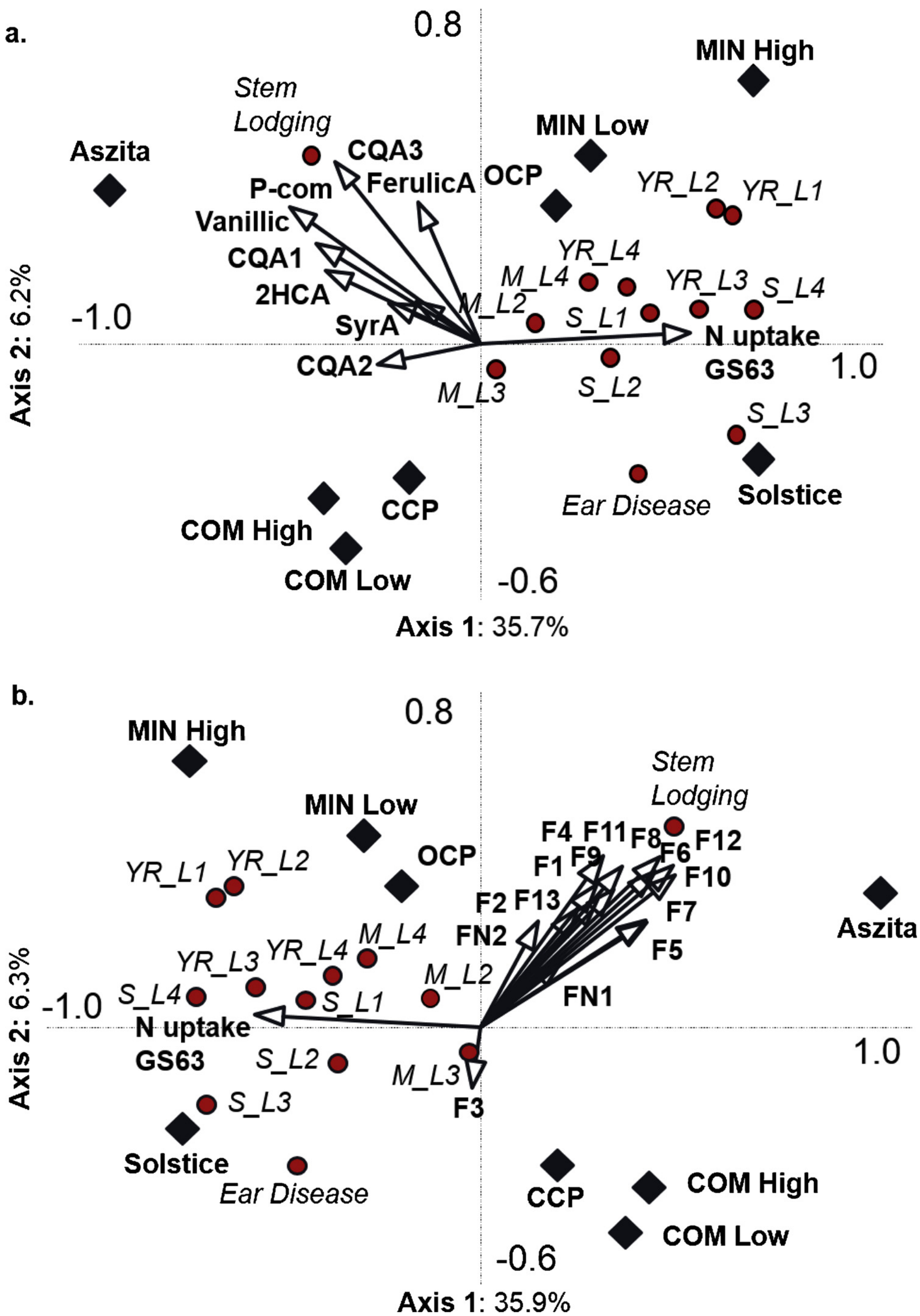

Fig. 3. Bi-plot derived from redundancy analysis showing: (a) associations between phenolic compounds and disease severity, (b) associations between flavonoids and disease severity (AUDPC) (see Table S7 for Monte Carlo permutation test values).
Arrows represent continuous explanatory variables/ drivers, while black diamonds represent explanatory variables/drivers. CCP: conventional crop protection; OCP: organic crop protection; COM: compost; MIN: mineral; CQA 1: neo-chlorogenic acid; CQA 2: chlorogenic acid CQA 3: 3´-methyl chlorogenic acid; SyrA: syringic acid; VanillicA: vanillic acid; *P*-com: *P*-coumaric acid; ferulic A: ferulic acid; 2HCA: 2-hydroxinnamic acid; F1: isoorientin 6″-O-xyloside; F2: mix of luteolin 6-C-galactoside 8-C-glucoside and lucenin-2 (luteolin 6, 8 di-C-glucoside); F3: apigenin 6-C-galactoside, 8-C-glucoside; F4: mix of uncharacterised apigenin and luteolin glycosides; F5: isoorientin; F6: isoorientin 2″-O-Rhamnoside; F7: 3´-C-glucoside, 2´,4´,6´,3,4-pentahydroxychalcone: F8: isovitexin; F9: isoscoparin (3´-methylluteolin 6-C-glucoside); F13: triticin; F10-f12: three uncharacterised flavonoid (flavones) peaks; S: Septoria; M: mildew; YR: yellow rust.

6.2% of the variation (Fig. 3a). Variety was identified as the strongest driver (*P* value = 0.02). Total plant N uptake at GS63, crop protection, CQA3, CQA2 and mineral fertilisation were also important drivers (*p* values between 0.002 and 0.006) (Table S7). Foliar and ear disease severity were positively associated with plant N uptake, use of the variety Solstice and mineral fertilisers and, to a lesser extent, the use of organic crop protection (OCP) along the positive axis 1. On the other hand foliar and ear disease was negatively associated with composted FYM fertiliser inputs, individual phenolic compounds and the use of the variety Aszita along axis 1 (Fig. 3a). Correlation analysis (which was performed separately for each variety) showed very similar trends (Fig. S7a, b). When associations between flavonoid compounds, agronomic and variety choice drivers/ explanatory variables, and disease severity were analysed by RDA (with climatic variables as supplementary drivers) very similar results were obtained (Fig. 3b) with correlation analysis also showing similar trends (Fig. S7a, b).

3.3. Grain yield, harvest index and crude protein content

Significant main effects of fertiliser input type, crop protection and variety (but not year) were detected for grain dry matter yield. Grain yield was higher when mineral fertiliser inputs, pesticide based conventional crop protection and the variety Solstice were used (Table 2). There were also significant 2-way interactions between: (a) year and fertility type; (b) fertility type and variety (Fig. S2) as well as significant 3-way interactions between: (a) year, fertility type and variety (Fig. 2c); (b) fertility type, crop protection and variety, which were further investigated (Fig. 2d). Fig. 2c and d describes the nature of the 3-way interactions detected for grain yield. Overall grain yields were higher in the warm/dry 2010 harvest year than the cool/wet 2012 harvest year.

However, when composted FYM was used as fertiliser, Aszita produced higher yields in the wet/cool 2012 season compared to 2010, while Solstice produced similar yields with composted FYM in both years (Fig. 2c). In contrast, when mineral N was used as fertiliser, both varieties produced higher yields in the dry/warm 2010 season, but the relative yield difference between years was greater for Solstice than Aszita (Fig. 2c). When composted FYM was used as fertiliser there was no significant difference between varieties and crop protection regimes. However, when mineral N-fertilisers were used the variety Solstice produced higher yields than Aszita, but only when conventional pesticide-based crop protection regimes were used; yields of the two varieties were not significantly different with organic crop protection (Fig. 2d).

Significant main effects of year, fertiliser input type, and variety (but not crop protection) were detected for harvest index (HI). HI was higher in the dry/warm season (2010), when mineral fertiliser inputs, and the variety Solstice were used (Table 2). There was also a significant 2-way interaction between year and variety (Fig. 2e) and a significant 3-way interaction between year, crop protection and variety (Fig. 2f). In the dry/warm season (2010) Solstice crops had significantly higher HI than Aszita, while both varieties had similar HI in the cooler/wet season (2012) (Fig. 2e). In the dry/warm season (2010) Solstice had significantly higher HI than Aszita when organic crop protection was used, while both varieties had similar HI when conventional crop protection (with growth regulators) was used (Fig. 2f). In contrast, in the cool/wet season (2012) Solstice had significantly higher HI than Aszita when conventional crop protection (which included treatment with the growth regulator chlormequat) was used while both varieties had similar HI when organic crop protection was used (Fig. 2f).

Significant main effects of fertiliser input type, fertiliser input level and variety (but not year and crop protection) were detected for grain crude protein concentrations (Table 2). Concentrations were higher when mineral N-fertiliser, the high fertiliser input level and the variety Aszita were used (Table 2). There were also significant 2-way interactions between: (a) year and fertility type (Fig. S3); (b) fertility type and fertility rate (Fig. S3); (c) year and variety (Fig. S3); (d) fertility type, variety (Fig. S3); € crop protection, variety (Fig. S3) as well as significant 3-way interactions between: (a) year, fertility type and variety (Fig. S3); (b) fertility type, fertility rate and variety (Fig. S3) and significant 4-way interactions between: (a) year, fertility type, fertility rate, variety (Fig. 2g); and (b) year, fertility type, crop protection, and variety (Fig. 2h).

The nature of the 4-way interactions between year, fertiliser type, fertiliser input level and variety detected for grain protein content is further described in Fig. 2g. In the dry/warm season (2010) Aszita crops produced significantly higher protein levels than Solstice in composted FYM fertilised plots when the lower composted FYM input level was used, while both varieties produced similar yields at the higher composted FYM input level (Fig. 2e). Protein levels for both varieties remained below the 11.5% required to obtain a baking quality premium in Europe. However, when mineral fertilised crops were compared in 2010, Aszita produced significantly higher protein levels than Solstice at both fertiliser input levels (Fig. 2g) and protein levels of Aszita (but not Solstice) were above the 11.5% protein required to obtain a baking quality premium.

In contrast, in the cool/wet season (2012) Aszita produced significantly higher protein contents than Solstice. Protein concentrations of Aszita were above the 11.5% baking quality threshold, while protein concentrations of Solstice were below 10% with all 4 fertilisation treatments (Fig. 2g). The nature of the 4-way interactions between year, fertiliser type, crop protection and variety detected for grain protein content is further described in Fig. 2h. In the dry/warm season (2010) no significant effect of using synthetic chemical fungicides, herbicides and growth regulators on protein content could be detected in both varieties when composted FYM was used as fertiliser (Fig. 2h). However, when mineral fertilised crops were compared in 2010, the use of conventional crop protection regimes resulted in slightly, but significantly higher protein concentrations in Solstice, but not Azsita (Fig. 2h). In contrast, in the cooler/wet season (2012) crop protection had no significant effect on protein levels in both varieties grown with either mineral or composted FYM fertilisers (Fig. 2h).

4. Discussion

The majority of studies aimed at quantifying effects of contrasting agronomic protocols (rotation design, fertilisation and crop protection) used in organic and conventional farming on winter wheat yield and quality were carried out using short straw varieties developed for the high input conventional sector (Bilsborrow et al., 2013; Cooper et al., 2011; Rempelos et al., 2018; Tetard-Jones et al., 2013). However, it has been suggested that these "conventional" wheat varieties may lack many important traits such as nutrient use efficiency from organic fertiliser inputs, competitiveness against weeds, and disease resistance necessary for optimum performance (e.g. grain yield, yield stability and quality) required for high performance in organic farming systems (Lammerts van Bueren et al., 2010; Lammerts van Bueren and Myers, 2012; Lammerts van Bueren et al., 2008; Lammerts Van Bueren et al., 2007; Murphy et al., 2007). This study is therefore one of the first to: (i) compare the performance of two winter wheat varieties, developed via conventional and organic /low-input farming focused breeding/selection programmes under contrasting fertilisation and crop protection protocols; (ii) identify interactions between variety, fertilisation and crop protection protocols with respect to leaf phenolic/flavonoid compound concentrations and their relationship with resistance against certain foliar fungal diseases; as well as (iii) assess the relative importance of genetic and agronomic factors/drivers for phenolic profiles, and crop health and performance parameters using redundancy analyses.

4.1. The importance of interactions between genetic and agronomic factors on leaf phenolic concentration and disease severity

The finding that both phenolic acid and flavonoid concentrations in flag leaves were substantially higher when composted FYM rather than mineral N is used at similar total N-input levels confirms results of our previous studies which investigated the effect of contrasting rotation, fertilisation and crop protection regimes on crop health, yield and quality parameters in the short straw variety Malacca, which was developed for and widely used in UK conventional farming systems in the past (Bilsborrow et al., 2013; Rempelos et al., 2018). Our findings are also consistent with other studies which reported negative correlations between mineral N-fertiliser input levels and phenolic acid and flavonoid content (Sander and Heitefuss, 1998; Siranidou et al., 2002), and studies which showed higher antioxidant/polyphenol concentrations in organic compared to conventional food and feed crops (Baranski et al., 2014).

The metabolism of phenolic and other antioxidant compounds in plants is known to be affected by climatic conditions and often reduced at low temperature and radiation levels (Agati et al., 2011; Del Rio et al., 2013; Fernandez-Orozco et al., 2010; Kim et al., 2012). The evolution of phenolic compounds in plants is believed to be a result of a "Trade-off" between growth and defence-related metabolism. Normally, when plant growth is more limited than photosynthesis, there will be an increase in resource allocation to carbon-based secondary defence compounds (Bryant et al., 1983; Coley et al., 1985; Herms and Mattson, 1992). It has also been suggested that the level of many phenolic compounds is low under some environmental conditions simply because the risk of photo damage is low and they are therefore not required (Close and McArthur, 2002). Results in this study suggest that the effect of warm/dry/high solar radiation conditions was greater for flavonoids (4 times higher in 2010 compared to 2012) than for phenolic acids (50–80% higher in 2010 than 2012). The finding that variety choice and fertilisation had substantial effects on phenolic concentrations only in the dryer/warm 2010 season, but not in 2012 indicates that genetic and agronomic regimes used in the present study cannot alleviate the negative effects of cool/wet/ low solar radiation weather conditions.

Results also suggest that Aszita (a variety developed for the organic/ low input farming sector) had a greater genetic potential for expression of high foliar phenolic concentrations than Solstice (a variety developed for the conventional farming sector). However, to our knowledge neither organic nor conventional programmes breed/select for high antioxidant/ (poly)-phenolic content. The overall higher phenolic concentrations found in Aszita may however, have resulted indirectly from the approaches taken in the organic breeding programmes, which focused on making crosses that are likely to result in longer straw, high levels of resistance against lodging/stem base diseases and/or applying stronger selection pressure for foliar disease resistance.

Semi-dwarfing genes were introduced into modern wheat varieties to reduce the risk of lodging and increase harvest index. However, in organic systems the non-use of mineral N-fertilisers results in a substantially lower incidence/risk of lodging, but also a reduction in protein content (Rempelos et al., 2018). Organic farmers are therefore able to and often choose longer-straw varieties, since straw length is often positively correlated with *Septoria* resistance, weed competitiveness and protein content (Lammerts van Bueren et al., 2010; Mayer et al., 2015).

The higher *Septoria* resistance/tolerance in longer straw varieties may be particularly important, since Septoria was reported to be the only foliar disease that that contributes to the yield gap between organic and conventional wheat production systems (Bilsborrow et al., 2013; Mayer et al., 2015). However, until a larger number of varieties/ genotypes from organic and conventional farming focused breeding/ selection programmes has been compared it remains unclear whether the differences between Aszita and Solstice represent a general trend or are specific to these two varieties.

Phenolic acids and flavonoids are thought to be involved in plant tolerance/ resistance to pests and diseases (Du Fall and Solomon, 2011) and selection for resistance against foliar and stem base diseases/lodging may therefore have resulted in co-selection for high genetic potential to produce high levels of phenolic compounds in leaves. This view would be consistent with the findings that redundancy analysis showed strong negative associations between foliar phenolic concentrations and both yellow rust and *Septoria* severity. Links between phenolic concentrations and resistance to foliar diseases in wheat such as powdery mildew and *Fusarium* have previously been reported (Atanasova-Penichon et al., 2016), but this is to our knowledge the first report of an association with *Septoria* resistance.

The finding that *Septoria* severity was higher, and yellow rust was only detected in Solstice, could lead to the conclusion that the lower disease susceptibility in Aszita might be caused by the higher concentrations of phenolic acids and flavonoids measured in this variety compared with Solstice. However, substantially higher phenolic concentrations in Aszita were only found in composted FYM fertilised plots, while the significant difference in *Septoria* severity (L2) between the two varieties were only detected in mineral fertilised crops (in both years) in which phenolic concentrations were not substantially different. This suggests that factors other than phenolic concentrations might have contributed to the difference in foliar disease severity between the two varieties.

Several studies reported that *S. tritici* severity is negatively correlated with plant height (Camacho-Casas et al., 1995; Danon, 1982) and it has been suggested that this could result from (a) unfavourable environmental and epidemiological factors due to plant height (Bahat et al., 1980; Scott et al., 1985; Simon et al., 2005), (b) the linkage between resistance and plant height (Scott et al., 1985), (c) the vertical transport of the pathogen from soil or infected lower leaves (Bahat et al., 1980; Eyal, 1981; Scott et al., 1985), as well as (d) the rate of stem extension. It was previously reported that the spore transfer to the upper leaves is affected by the rate of stem extension which is a major reason for the rapid spread of disease from inoculum on the lower leaves to the upper leaves and flag leaf in short straw varieties (Lovell et al., 1997). This could therefore also explain the difference in disease severity between the two varieties, however more evidence from studies comparing *S. tritici* resistance between long and short straw wheat varieties is required.

Breeding and selection regimes used for organic bread making wheat varieties often generate varieties with a (1) longer straw, which is known to be positively correlated with improved *Septoria* tolerance as well as protein content (Dotlačil et al., 2011; Scott et al., 1985); (2) high *Septoria*, rust and bunt resistance, (3) high yield and nutrient uptake efficiency from organic fertiliser inputs and (4) high protein content and bread making quality (Crespo-Herrera and Ortiz, 2015; Lammerts van Bueren et al., 2010, 2008; Wolfe et al., 2008). However, the effect of organic vs conventional breeding and selection regimes on phenolic profiles and concentrations has, to our knowledge, not previously been studied.

4.2. The relative importance of the interactions between agronomic and genetic factors on wheat grain yield and crude protein concentrations

The overall 30% higher yield in in the warmer/dryer 2010 season was not surprising, since seasons with relatively high temperatures and solar radiation and, moderate rainfall tend to result in the highest yields. However, the finding that substantial differences in yield between the two seasons and between the two varieties could only be detected in mineral fertilised crops was unexpected. In fact, Aszita had numerically higher yields than Solstice in the cooler/wetter 2012 season when composted FYM was used as fertiliser, and Solstice significantly higher yields in the warmer/dryer 2010 season only when mineral N-fertiliser was used.

It could hypothesise that the yield differences between the two seasons were likely due to greater N-losses especially in mineral-N fertiliser plots in 2012 because of the 3 times higher rainfall (131 mm vs 517.6 mm) between April and August in 2012. However, the total N-uptake at anthesis in 2012 (cool/wet season) were higher than in 2010 (data not shown), which suggests that factors other than N-availability may have contributed, to the lower grain yield in 2012. It is likely that the 30% lower solar radiation during the 2012 post-anthesis (grain filling) period was a key yield limiting factor. Grain filling depends on both stem dry matter reserves and solar radiation (and associated levels of photosynthesis), and known to be an important factors regulating winter wheat yields (Murchie et al., 2009; Xiong et al., 2012). Stem dry matter reserves are thought to have a limited effect on yield formation. However, under environmental stress pre-anthesis dry matter reserves were shown to make a larger contribution to yield formation (Bidinger et al., 1977). The may explain the finding that in 2012 (the wet/cold season) the long straw variety (Aszita) showed a 25% reduction in HI compared to 2010 while the short straw one (Solstice) a 40% indicates that stem length might also play a role in stem dry matter reserves and its translocation during grain filling under stress conditions.

Grain yield is often reported to be negatively correlated with protein content due to a yield dilution effect (McDonald et al., 2008). However in our study correlation analysis showed a strong positive correlation between yield and protein only in warm/ dry 2010. It is therefore surprising that grain protein levels in the composted FYM fertilised Aszita were higher in 2012 (the wet/cold season with low solar radiation) than 2010. Previous studies suggest that this may have been linked to (a) differences in the root system development, (b) increased N uptake during later stages of grain filling, and/or (c) variation in the N translocation efficiency leading to a higher protein content in vegetative tissues, and a larger protein reservoir at the onset of grain filling (Kramer, 1979). In the present study, both varieties were planted on the same date and reached different growth stages and maturity at the same time. This makes it unlikely that differences in the speed of development between varieties affected N-uptake. However, root system development was not monitored and may have differed between varieties. Future studies should therefore investigate differences in root systems and development pattern between varieties from contrasting breeding programmes.

It should also be pointed out that average yield levels for both varieties were relatively low compared to average winter wheat yields achieved at Nafferton farm both in commercial production and the long-term field experiments under similar organic and conventional fertilisation and crop protection regimes (Bilsborrow et al., 2013; Cooper et al., 2011; Swain et al., 2014; Tetard-Jones et al., 2013). This is thought to have been due to (a) experiments having been established mid-rotation (after two years winter cereal crops and an oilseed rape crop) resulting in a low nutrient and especially N_{min} status; (b) exceptionally poor weather conditions in 2012 when commercial wheat yields in the North East of England were at record low levels and (c) the fact that no P and K fertiliser was applied to the mineral N fertility input type plots. Results suggest that Solstice was the variety with the higher yield potential, but that this potential is only realised in mineral-N fertilised plots and in the dryer-warmer 2010 season. It is interesting to note that Solstice responded to switching from composted FYM to mineral fertiliser inputs with a larger relative yield, but lower relative protein increase than Aszita (protein contents in Solstice remained well below the threshold required for baking quality in the UK in both seasons i.e. 13%), which was also likely to have been due to the contrasting agronomic backgrounds and selection criteria used during breeding/selection of the two varieties.

Solstice would be expected to deliver higher economic returns than Aszita in intensive conventional farming systems but the low protein concentrations (< 10%) in both seasons suggest that it is an unsuitable variety for production of bread-making quality wheat in the North of England. On the other hand Solstice did not achieve its yield potential under the cool wet conditions experienced in 2012 as well as the composted FYM fertilised plots in both seasons (conditions under which no difference in yield between the two varieties was detected). This clearly indicated that Solstice delivers the primary target traits of conventional UK wheat breeding programmes such as short straw and associated lodging resistance and high grain yield under optimised mineral fertiliser and crop protection input regimes. However, it should be pointed out that the increase in Solstice yield from herbicide, fungicide and growth regulator applications in mineral fertilised crops was not significant. Results also indicate that the yield potential of Solstice cannot be realised (a) under organic farming conditions where average annual N-inputs with organic fertilisers are restricted to an average of 170 kg ha^{-1} $year^{-1}$ (= the higher manure input level used in this study), and (b) in cooler seasons with high rainfall, which may affect N-supply to crops by increasing run-off and leaching of mineral N-fertilisers), and low solar radiation (=low photosynthetic activity), which may affect grain filling and therefore reduce grain yields.

Aszita had the same yields in both seasons but higher protein concentrations than Solstice and in 2012 protein concentrations in composted FYM fertilised Aszita crops were above the threshold of 11.5% set for organic baking quality premiums. Aszita also had higher levels of *Septoria* resistance, which is the main disease affecting wheat crops in the UK, and for which no effective crop protection treatments are available for organic farmers. The use of Aszita is therefore expected to deliver higher yield stability (less variable yields in seasons with contrasting climatic conditions) and economic returns under organic farming conditions, especially if the farmer aims at supplying the bread-making wheat market. However, future studies should investigate if varieties that are bred for organic and low input systems have higher nutrient uptake and use efficiency leading to greater yield stability especially in seasons with extreme climatic conditions.

5. Conclusions

Since this study only compared one modern, short-straw variety (Solstice) with one longer-straw variety from an organic farming focused breeding program (Aszita), results obtained cannot be used to draw general conclusions on the outcomes of contrasting breeding/selection protocols used for the conventional or organic/low input farming sector. However, the results from this pilot study provides for the first time some evidence that customizing breeding/selection protocols to the needs of specific production systems may deliver varieties that are more adapted to the farming sector targeted. These results should be confirmed in future studies comparing a wider range of varieties from both conventional and organic/ low-input breeding programmes.

Apart from greater foliar disease resistance, the “organic” variety Aszita produced higher grain protein levels, which may both be linked to the greater stem length targeted in organic breeding programmes. In contrast, conventional farming focused breeding programmes select for high yields under high mineral fertiliser input regimes and therefore target shorter stems, due to the higher lodging risk when high mineral-N inputs are used. Furthermore, *Septoria* was confirmed as the main foliar disease affecting yields in organic production systems, while in conventional crops a wider range of obligate fungal pathogens (such as *Fusarium*, rusts and powdery mildew) were observed in addition to lodging, which can be exacerbated by high mineral-N fertiliser inputs may cause substantial yield losses. Our results therefore also indicate that the greater yield potential of varieties bred for the conventional farming sector may only be realised with high N- fertiliser and pesticide inputs.

The expression of enzymes involved in the biosynthesis of phenolic compounds was recently shown to differ considerably between wheat varieties and different development stages of wheat, and phenolic concentrations in wheat tissues may affect the expression of genes involved in phenolic biosynthesis and/or metabolism (Boutigny et al., 2010). In addition, phenolic compounds were shown to affect the expression of genes involved in mycotoxin biosynthesis in *Fusarium* spp. (Ma et al., 2016). The differential expression of specific genes in different wheat genotypes, at key developmental stages, and under contrasting environmental conditions has the potential to contribute to the identification of functional molecular markers to aid future wheat breeding programmes. It is therefore important to further elucidate the role of fertilisation regimes and phenolic/flavonoid compounds as regulators of gene expression in plants and pathogenic fungi. Future studies should investigate whether and to what extent the higher foliar phenolic levels are linked to disease resistance in Aszita/other long straw varieties, and whether phenolics are present in the grain, as these compounds are mainly localized to the outer layers of the grain and have been linked to the positive effects of whole grain consumption.

Future breeding programmes for the low input and organic sector should therefore focus on increasing yield potential under organic fertilisation regimes e.g. by focusing on traits such as high N-scavenging capacity and N use efficiency from organic fertiliser inputs as well as *Septoria* resistance. In contrast, breeding for conventional farming systems need to continue to focus on breeding for resistance to a wider range of foliar pathogens, high phenolic expression under high mineral N-input regimes, especially if these compounds are confirmed as resistance factors and/or being nutritionally-desirable.

CRediT authorship contribution statement

Leonidas Rempelos: Methodology, Investigation, Formal analysis, Data curation, Visualization, Writing - review & editing. **Mohammed Saleh Bady Almuayrifi:** Methodology, Investigation, Writing - review & editing. **Marcin Baranski:** Investigation, Data curation, Visualization. **Catherine Tetard-Jones:** Methodology, Supervision. **Bronwyn Barkla:** Writing - review & editing. **Ismail Cakmak:**

Conceptualization, Funding acquisition, Investigation. **Levent Ozturk:** Funding acquisition, Investigation. **Julia Cooper:** Project administration, Supervision, Writing - review & editing. **Nikolaos Volakakis:** Resources, Investigation. **Gavin Hall:** Resources, Investigation. **Bingqiang Zhao:** Conceptualization, Funding acquisition, Project administration, Writing - review & editing. **Terry J. Rose:** Writing - review & editing. **Juan Wang:** Writing - review & editing. **Hassan A. Kalee:** Writing - review & editing. **Enas Sufar:** Writing - review & editing. **Gultakin Hasanalieya:** Writing - review & editing. **Paul Bilsborrow:** Supervision, Writing - review & editing. **Carlo Leifert:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fcr.2020.107822.

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