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Published in:
Field Crops Research

DOI:
10.1016/j.fcr.2019.04.020

Print publication: 01/06/2019

Document Version
Peer reviewed version

In sink-limited spring barley crops, light interception by green canopy does not need protection against foliar disease for the entire duration of grain filling

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Abstract

Disease management in cereals is heavily reliant on the use of fungicides, but development of anti-microbial resistance, effects on non-target organisms and persistence of active ingredients in the environment and food chain challenge the sustainability of this approach. Better targeting of fungicides according to crop need within an integrated pest management (IPM) programme could improve the sustainability of disease management. The objectives of the present study were to determine 1) the duration of protection of post-anthesis canopy light interception required to maximise the yield of spring barley and 2) to relate this to the response of crops to timing of fungicide applications. As the yield of spring barley is considered to be sink-limited (limited by the number and storage capacity of grains) rather than source-limited (limited by the amount of carbon assimilates available for grain filling) in many environments, we hypothesised that the canopy would not need to be protected for the entire grain filling period. Field experiments were conducted at two sites in the UK (Edinburgh and Herefordshire) over four years, providing contrasting climates and soil types. Shading was used to determine the response of grain filling to reductions in light interception over defined intervals, thereby mimicking effects of foliar disease on light interception, as shading is easier to control than the onset and duration of disease epidemics. Shades giving ~67% reduction in photosynthetically active radiation (PAR) were erected over plots of disease-free crops at weekly intervals commencing at flowering and leaving them in place until harvest. The required duration of protection of light interception was estimated as the period from flowering to the time at which the onset of shading had no effect on yield. In a separate experiment the response to five fungicide timing treatments was determined on three relatively disease-susceptible varieties. Timings were the start of stem extension (referred to here as T1 only) and T1 followed by a second application at either flag leaf emergence (early T2), flowering (mid T2) or the start of rapid grain growth (late T2); untreated plots served as controls. Results showed that canopy PAR interception does not need to be protected for the entire grain filling period in order to maximise yield. The critical period determined from shading was 3-5 weeks after 50% ear emergence depending on the site year, or the first 72-90% of

grain filling. There was a significant yield response to fungicide treatment in all site-years of 0.33-0.74 t ha^{-1} irrespective of the disease severity and yield potential of the site. Where disease severity was low to moderate a T1 application on its own gave sufficient protection during grain filling to maximise yield. Later applications increased healthy area PAR interception further, but effects occurred late during grain filling and did not increase yield. When disease was severe a T1 plus mid T2 application was required to protect PAR interception during the critical early to mid- grain filling period. These results provide the necessary physiological understanding to help target fungicide applications according to crop need.

Key words: fungicide timing; *Hordeum vulgare*; integrated pest management (IPM); shading; yield.

1. Introduction

Yield loss to disease in the major cereal crops averages from around 9 to 11% depending on the species, representing approximately 335 Mt of total global production annually (Oerke, 2006). Fungicides are the mainstay of disease management programmes in these systems with 418,000t of fungicide and bactericide active ingredient applied in 2014 (FAOstat 2018).

The rational use of fungicides requires that they only be applied to crops where there is likely to be an economic increase in yield or quality (Jorgensen et al., 2017). Improved targeting, based on a consideration of the crop's likely response to disease control, could lead to a reduction in the number of treatments made, or their dose, with potential benefits for the sustainability of disease management (Bingham et al., 2009; Ney et al., 2013; van den Berg et al., 2013). A better understanding of the physiological effects of disease on the yield forming process would allow treatments to be targeted at those stages in the crop's lifecycle where protection is most critical.

Yield formation in wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) is a season long process (Slafer et al., 2014). Crop growth and development before flowering determines the size of the canopy established and the crop's grain sink capacity. The sink capacity is a function of both the

number of grains produced, as governed by the production and survival of tillers and spikelets, and their potential size (individual storage capacity). Post-anthesis photosynthetic activity, and the remobilization of soluble carbohydrate reserves stored pre-anthesis, supply the carbon assimilates for grain filling.

Foliar disease can impact on crop growth through effects on radiation interception, radiation use efficiency and biomass partitioning to sink tissues, although for many pathogens effects on radiation interception dominate (Bingham et al. 2009). The impact on yield will depend on the timing of the disease epidemic, its location in the canopy and the relative source-sink balance of the crop (Gaunt, 1995, Bingham et al. 2009; Bingham and Topp 2009). Hence, although yield formation is a season-long process, it does not follow that protection from disease is required from crop emergence to senescence.

Although yield of wheat is considered to be sink-limited in a number of environments (Borras et al., 2004), in the light-limited conditions of the UK source and sink capacities are in close balance (Beed et al., 2007). The effects of foliar disease on the development of sink capacity are small relative to effects on photosynthetic activity during grain filling. The emphasis of disease management in UK wheat is, therefore, on post-anthesis canopy protection to maximise canopy duration (i.e. post-anthesis canopy lifespan) and assimilate supply for grain filling (Bryson et al., 1997; Paveley et al., 2001).

By contrast there is evidence that yield of winter and spring barley, even in high yielding environments, is largely sink-limited (Bingham et al., 2007; Kennedy et al., 2017). Thus, the aim in barley is first to maximise the development of grain sink capacity and then to protect the canopy post-anthesis to ensure there is enough assimilate available to meet the sink demand. However, the duration of protection of canopy photosynthetically active radiation (PAR) interception required during grain filling of barley has not been quantified and thus we have a poor mechanistic understanding on which to base decisions regarding fungicide timing. The research reported here used two experimental approaches to determine for how long during the grain filling period canopy

PAR interception must be protected in order to maximise yield, and to relate the duration of protection required to the response of yield to fungicide timing. We hypothesised that because yield of barley is typically sink-limited, canopy PAR interception does not need to be protected for the entire grain filling period and that maximising green area duration with late fungicide timing is unnecessary.

2. Materials and Methods

2.1 Experimental rationale

To test the hypothesis, two experimental approaches were used; referred to as 'fungicide timing experiments' and 'shading experiments'. All experiments were conducted under rain-fed conditions.

In the fungicide timing experiments, three disease susceptible varieties of spring barley were grown and a range of fungicide timings used to manipulate the duration and timing of post-anthesis disease epidemics. The rationale was that an early fungicide applied at the start of stem extension (GS 30/31; referred to here as timing T1) would be expected to provide relatively little protection during the post-anthesis period. A second application applied 2, 4 or 6 weeks later (broadly equivalent to GS37, GS49/55 and GS71, respectively) would give protection of the canopy progressively later into the grain filling period. An assessment of the effects of the different fungicide timings on disease severity, percentage green leaf area and healthy (green) area PAR interception and their relationship to grain yield could then be interpreted in terms of the critical period of canopy protection required.

It is impossible to start and stop a disease epidemic in the field at precise timings by the use of fungicides. This limits the precision with which the duration of canopy protection required can be quantified. Hence, in a second series of experiments, crop shading was used to reduce canopy PAR interception over precise intervals, as a proxy for foliar disease reducing canopy PAR interception. The rationale for this is described below. Fungal pathogens, especially necrotrophs and hemi-biotrophs, reduce plant growth largely through their effects on radiation interception (Bingham et al., 2009). Chlorotic and necrotic lesions associated with visible disease symptoms reduce the healthy area available for PAR interception. PAR falling on senescent and dead leaf tissue is effectively 'lost' and

unavailable for photosynthesis. Shading was used as a proxy for the effects of disease on post-anthesis PAR interception. Interception by green canopy was reduced by PAR hitting shade netting, as a proxy for PAR hitting necrotic lesions. The shade netting could be put in place and removed at precise timings. Commencing at 50% ear emergence (Zadoks growth stage (GS) 55; Tottman and Broad, 1987) shade netting was erected over plots of spring barley at successive weekly intervals and left in place until harvest (Fig. 1). Disease was prevented by using a variety 'Westminster' with good resistance to foliar disease and the application of a fungicide programme. The netting reduced incident PAR at the top of the canopy by 64-69%; equivalent to a severe disease epidemic. The duration of protection of canopy PAR interception required to maximise yield (the critical period for protection) was estimated as the period between GS 55 and the time at which the onset of shading had no significant effect on yield.

2.2 Fungicide timing experiments

2.2.1 Sites and experimental design

Experiments were conducted at ADAS, Herefordshire (52.34^{o}N 2.87^{o}W) in 2011 and SRUC, Boghall Farm Edinburgh (latitude 55.88^{o}N, longitude 3.20^{o}W) in 2011 and 2012. In all cases the previous crop was spring barley and the top soil texture was silty clay loam, pH 6.3, at the ADAS site and sandy loam, pH 5.8 (2011) and 6.0 (2012) at the SRUC sites. Plots (10 x 2 m) of spring barley were drilled at a viable seed rate of 350-360 seed m^{-2} on 22 March 2011 at ADAS and 21 March 2011 and 15 March 2012 at the SRUC sites. At ADAS the experiment was laid out in a randomised block design with 4 replicate blocks. Treatments consisted of 3 varieties (Optic and Forensic, two-row malting cultivars, plus Waggon, a two-row feed cultivar) and 5 fungicide timings (untreated, T1 only (GS30/31), T1 plus T2 at 2, 4 or 6 weeks after T1). At SRUC a split-plot design was used with 4 replicate blocks. Varieties were randomised within main plots and fungicide treatments in sub-plots. Fungicide treatments were prothioconazole (Proline at 0.4 l ha^{-1}) plus pyraclostrobin (Comet 200 at 0.63 l ha^{-1}) at both T1 and T2 timings. Fertilizer N was supplied as poultry manure at ADAS 2011 giving approximately 225 kg N ha^{-1}

(79 kg ha^{-1} readily available N). At SRUC in 2011 and 2012, N was supplied as ammonium nitrate at rates of 130 and 100 kg N ha^{-1} respectively (Sinclair et al., 2009; Defra 2010). Fertilizer P, K and S were applied according to soil mineral analysis and anticipated crop demand. Micronutrients, herbicides and insecticides were applied to all plots as required according to standard farm practice with the aim of avoiding nutrient deficiency and providing robust weed and pest control.

2.2.2 Measurements

Absolute area, % green area (GA) and disease severity were determined every two weeks commencing at GS 55 on ten shoots sampled at random per plot. Leaf laminae and stem were divided into fractions that corresponded to individual leaf layers, stem sections between successive leaves (incorporating stem and leaf sheath), peduncle and ear. Disease severity was assessed on the upper surface of each fully emerged leaf by estimating visually the % area occupied by sporulating and necrotic disease lesions, excluding the area of associated chlorosis. The latter was accounted for in a separate assessment of the % GA that considered both natural and disease-induced chlorosis and necrosis. Disease and % GA were assessed in the same way on each section of stem plus leaf sheath and on the peduncle and ear. Colour reference charts were used to standardise assessment of GA between SRUC and ADAS. After assessment of disease and % GA, the absolute projected area of each fraction (ear, peduncle, leaf laminae and stem plus leaf sheath layers) was determined using a leaf area meter (Li-Cor Biosciences, Lincoln, USA).

PAR interception by the canopy was determined within a day or two of disease sampling using a Sunscan Canopy Analysis System (Delta T Devices Ltd, Cambridge, UK). Simultaneous measurements were made of PAR above and below the canopy at nine locations along the length of the plot. To measure PAR at the base of the canopy the Sunscan probe was inserted at an angle of 45^{o} to the plant rows. Towards the end of grain filling sites were visited 3 times a week and the date of leaf and stem senescence was recorded when less than 5% of shoots had green area remaining on leaf laminae or stem respectively. Meteorological data were recorded continuously at each site. Plots were harvested

by small plot combine and yield measured on the combine. Grain samples were taken for determination of mean grain weight (MGW) and gravimetric moisture content. MGW was determined by counting the number of grains in an accurately weighed (to the nearest mg) sample of approximately 15 g. Yield and MGW are expressed on the basis of 100% dry matter after correcting for grain moisture content. Grain number m^{-2} was calculated as grain yield/MGW.

2.3 Shading experiments

2.3.1 Sites and experimental design

Shading experiments were conducted at ADAS Rosemaund, Herefordshire, UK (latitude 52.13°N, longitude 2.65°W) in 2009 and SRUC, Boghall Farm, Edinburgh, UK (latitude 55.88°N, longitude 3.20°W) in 2010 and 2011. In each case, fields occupied a rotational position that was representative of barley production in the region; at ADAS 2009 the previous crop was potatoes, whilst at SRUC it was spring barley. Top soil texture was silty clay loam at ADAS and sandy loam at SRUC with a pH of 6.9 and 5.8 respectively; lime was applied after soil analysis but prior to sowing at SRUC. Plots (10 x 2 m) of spring barley (*Hordeum vulgare* cultivar Westminster; a two-row feed cultivar with good disease resistance) were drilled at a viable seed rate of 360 seed m^{-2} on 13 March 2009, 16 March 2010 and 21 March 2011. Fertilizer N was applied as ammonium nitrate at rates recommended for high yielding malting barley crops based on previous cropping and/or soil analysis; 100, 110 and 100 kg N ha^{-1} were applied in 2009, 2010 and 2011 respectively (Sinclair et al., 2009; Defra 2010). Disease was controlled using prophylactic applications of prothioconazole (Proline at 0.4 l ha^{-1}) plus pyraclostrobin (Comet 200 at 0.63 l ha^{-1}) at GS 15/30 and GS 39/45. All other inputs were as described for the fungicide timing experiments

The experimental design was a complete randomised block with three replicate plots per shading treatment. Plots were drilled as close as possible to an east-west direction. Within a block, three discard plots were drilled between each experimental plot and a discard area exceeding 10 m in length sown between adjacent blocks. Discards were to prevent shadows being cast from shaded plots onto

non-shaded experimental plots both within and between blocks. Shortly before ear emergence, fence posts 1.5 m in height above ground level were erected around the plots. From GS 55 onwards shade nets (Haygrove Ltd, Ledbury, UK) were erected at weekly intervals over the designated experimental plot and its adjacent discard plots; control plots were left unshaded throughout grain filling. The netting was secured to a support structure of fence wire running between the posts. At the ends of the plots (E and W) the netting was secured below canopy height to prevent direct light penetrating under the shading when the solar zenith angle was large. Along the N and S edges, the netting was secured 1.2 m above ground level to provide adequate ventilation under the shade, whilst preventing ambient light reaching the experimental plot. The netting was constructed of an open mesh of black polyethylene, which allowed rainfall to penetrate whilst restricting transmission of photosynthetically active radiation (PAR).

2.3.2 Measurements

At weekly intervals starting from GS55, 20 shoots were sampled at random from the length of unshaded control plots. Shoots were separated into three fractions; leaf laminae, stem plus leaf sheaths and ears and each fraction dried in a fan assisted oven at 80^{o}C for 48h for dry weight determination. Disease severity and % green leaf area (GLA) were assessed visually every two weeks commencing at GS55 on ten shoots sampled at random from each of the shaded and unshaded plots. Shoots were cut at ground level, sealed in a polythene bag to prevent moisture loss and transferred to the laboratory for assessment. Samples were assessed immediately or stored in their plastic bags in the dark at 4^{o}C for up to 48 h.

The reduction in PAR incident on the canopy as a result of the shading was quantified by measuring incident PAR above the canopy simultaneously in shaded and unshaded plots using a Sunscan Canopy Analysis System (Delta T Devices Ltd, Cambridge, UK). The shading reduced incident PAR by 64-69% depending on the site and varied little over the course of grain filling. Differences between sites probably reflect small differences in the tension applied to the netting over the support

structures. Temperature, relative humidity and rainfall were logged continuously under the shade and in an adjacent unshaded area. Soil cores to 90 cm were taken every two weeks from shaded and unshaded discard plots for determination of gravimetric soil moisture content. Cores were divided into 30 cm depth intervals, stones removed by hand and gravimetric water content determined after drying the soil at 100^{o}C for 48h. At harvest maturity, shades and posts were removed and plots harvested by small plot combine. Yield was measured on the combine and a sample taken for gravimetric determination of grain moisture content to correct yield measurements. Yields are expressed on the basis of 100% dry matter.

2.4 Calculations and statistical analysis

PAR interception by healthy tissue was estimated using methods adapted from Bingham et al. (2012). A canopy area index (CAI, total projected area per unit ground area) was calculated from the measurements of incident and transmitted PAR using Beer's law analogy assuming a light extinction coefficient (k) of 0.5 (equation 1):

$$CAI = [\ln (I_t/I_o]/k \quad (1)$$

where I_o is the incident PAR and I_t is the PAR transmitted to the base of the canopy.

Measurements of absolute ear, leaf and stem plus leaf sheath area were used to calculate the proportional distribution of projected area in five zones representing the ear and top five leaf layers. The projected (planar) area for a particular leaf layer was given by the sum of the lamina area in that layer and the stem (plus leaf sheath) section between the leaf and the one above it. In the case of the flag leaf layer (leaf layer 1), the area consisted of the leaf lamina plus the peduncle. The stem below leaf five plus any remaining senesced non-culm leaves were included in the leaf 5 layer. The ear comprised an additional layer. The projected area in each layer was then expressed as a fraction of

the sum of all layers. The fractional distribution of projected area from the measured samples was used to estimate the *CAI* in each layer as (equation 2):

$$CAI_h = CAI \times fLA_h \quad (2)$$

where CAI_h is the *CAI* of layer *h* and fLA_h is the projected area of layer *h* expressed as a fraction of the total area.

PAR intercepted by each layer was then calculated as:

$$I_h = I_{0h} \times [1 - \exp(-k \times CAI_h)] \quad (3)$$

where I_h is the PAR intercepted by layer *h*, I_{oh} is the PAR incident on layer h, and *k* is the assumed extinction coefficient of 0.5. I_{oh} was calculated as the difference between the daily amount of PAR incident on the top of the canopy and the sum of that intercepted by all layers above layer *h*.

The PAR intercepted by healthy (green) tissue in a given layer h was then given as:

$$HA_{inth} = I_h \times [HAI_h/CAI_h] \quad (4)$$

where HA_{inth} is the healthy area PAR interception by layer *h* and HAI_h/CAI_h is the fraction of the canopy area index in layer *h* that is healthy (green). The latter was calculated from a weighted average of the measured % GA values of leaf lamina and stem plus leaf sheath for the layer in question; for the ear layer it was calculated from the measured %GA of the ear on its own

HA_{int} for the canopy as a whole was calculated as the sum for the individual leaf and ear layers and expressed as the fraction (F_{PAR}) of the incident PAR for the day ($I_0\ day$):

$$F_{PAR} = HA_{int}/I_0\ day \quad (5)$$

To estimate HA_{int} over a given interval between growth stages, the value of F_{PAR} for each of the bounding growth stages was averaged and multiplied by the sum of the daily incident PAR for the interval. The above method of estimating PAR interception by healthy (green) tissue takes into account the distribution of disease within the canopy. It also assumes that PAR incident on necrotic and chlorotic tissue is intercepted and not reflected or transmitted to neighbouring green healthy tissue.

By using measured values of PAR transmission through the canopy and the distribution of projected and healthy tissue area by layer from random shoot samples, this method of estimating HA_{int} avoids the need for time-consuming quadrat sampling and direct measurement of *CAI*. The assumed value of light extinction coefficient (*k*) used in the calculations is not critical, because the value is first used to estimate the *CAI* from incident and transmitted PAR in equation 1 and the same value is then used in the reverse calculation in equation 3 to estimate the amount of PAR intercepted by each layer.

The duration of grain filling was estimated from the progress of ear dry weight of unshaded crops against accumulated ^{o}C days from GS55 assuming a base temperature of 0^{o}C. The end of grain filling was taken to be the point when maximum ear weight was attained. Post anthesis shading has been shown to have little effect on the duration of grain filling in spring barley (Kennedy et al., 2018). Interpolation of these data was used to estimate the fraction of grain filling completed at specific times (^{o}Cd) after GS55).

Statistical analysis was by ANOVA for randomised block or split-plot designs using Genstat 14th Edition (VSN International Ltd., Hemel Hemstead, UK). Residuals were checked for homogeneity of variance and normality of distribution and transformed where necessary. Percentage values for individual diseases and disorders were arcsine transformed prior to analysis. Back-transformed mean values are presented. Split-line regression (Genstat 14th Edition) was used to determine the

breakpoint in the relationship between grain yield and time of shading. A bilinear model with a plateau was fitted as:

$Y = a + bx$, if $x<c$; $Y = a + bc$, if $x \geq c$;

Where Y is grain yield; a is the Y-intercept; b is the slope; x is the time after GS55 when shades were erected (taken to be time after anthesis) and c is the critical period of canopy protection (the break point). A bilinear model with plateau was also fitted to plots of post-anthesis HA_{int} against yield from the fungicide timing experiments; here Y is grain yield; a is the Y-intercept; b is the slope; x is the post-anthesis healthy area PAR interception (HA_{int}); c is the HA_{int} above which there is no further increase in yield.

3. Results

3.1 Weather conditions

The average daily temperature and monthly rainfall data for the different sites and years are shown in Fig. 2. On the whole, temperatures followed the long term average for the sites in 2009 to 2011. At both ADAS and SRUC in 2011, the temperature was slightly higher (2-3^{o}C) than average in April and lower (~1.0-1.5^{o}C) in June to August. Temperatures throughout the growing period were lower at SRUC than ADAS reflecting the more northerly latitude of the SRUC site. This was associated with a slower rate of crop development at SRUC in which the date of ear emergence was 7 to 10 days later and harvest 7-15 days later than at ADAS. In 2012, the temperature was lower than the long term average for most of the growing season.

Overall 2009 and 2011 at ADAS and 2010 at SRUC were drier than average years, with the exception of July (and June at ADAS 2009) which had average to above average rainfall. By contrast 2011 and 2012 at SRUC were characterised by having exceptionally wet summer months. For example between April and August 2012, the total rainfall was nearly three times the long term average.

3.2 Response to fungicide timing

3.2.1 Disease severity on susceptible varieties

Three relatively disease susceptible varieties were grown and fungicide timing used to vary the severity of disease around flowering and during grain filling. The type and severity of visible disease or disorder present on untreated crops after flowering differed between sites and varieties (Fig. 3). At ADAS in 2011, the main diseases were powdery mildew (*Blumeria graminis* f.sp. *hordei*) and rhynchosporium leaf scald (*Rhynchosporium commune*); severities were low to moderate (<8%) and each variety was affected to a similar extent. Variety Waggon possess the *mlo* allele conferring powdery mildew resistance. Since disease was scored as the area of sporulating lesions and necrotic tissue, the small amount of mildew recorded probably represents necrotic tissue resulting from a hyper sensitive response. At SRUC in 2011, the severity of mildew and rhynchosporium was also low to moderate (<6%), but at this site Waggon developed significantly less disease than Forensic or Optic. However, the greatest loss of green area resulted from physiological brown spotting and here Forensic was the cultivar most severely affected (>10% leaf area). At SRUC in 2012, which was exceptionally wet for most of the growing season, there was a major ramularia leaf spot (*Ramularia collo-cygni*) epidemic with average severities exceeding 30% of the leaf area for all varieties

3.2.2 Grain yield and yield components

Yield differed widely between site-years ranging from around 3.15 t ha^{-1} for untreated crops at SRUC 2012 (averaged across varieties) to 6.49 at ADAS 2011 (Table 1). In each of the three site-years yield increased ($P<0.001$) by 0.33 to 0.74 t ha^{-1} in response to fungicide treatment (Table 1). At ADAS 2011 and SRUC 2012 there was no significant interaction ($P>0.05$) between variety and fungicide treatment indicating that varieties responded to fungicide in the same way. This is consistent with the relatively small differences in disease severity between varieties at these sites. At SRUC in 2011, there was a significant interaction ($P<0.05$) with Waggon showing no overall response to fungicide, in contrast to Optic and Forensic, consistent with the lower severity of disease and spotting observed on Waggon.

Averaged across varieties, an application of fungicide at GS30/31 (the T1 timing) gave a significant yield increase at all sites ranging from 6 to 10%. An additional application at T2 gave a further increase in yield only at SRUC 2012; the site-year where there was a severe ramularia leaf spot epidemic. Here the largest increase (~0.25 t ha^{-1}) was associated with an application at the mid or late T2 timing (4 or 6 weeks after T1; GS51/53 and GS71 respectively).

Differences in grain number m^{-2} and MGW contributed to the yield variation observed across sites and years (Table 1). In untreated crops grain numbers ranged from 14838 m^{-2} from the highest yielding site-year (ADAS 2011) to just 9130 m^{-2} for the lowest (SRUC 2012). MGW for untreated crops was broadly comparable (when averaged across varieties) for ADAS and SRUC in 2011 (~44 mg), but was approximately 33% lower at SRUC in 2012. In all site-years fungicide treatment resulted in a 3-6% increase in grain numbers. These increases were significant ($P<0.05$) only at SRUC. In 2011, the application at T1 contributed most to the increase, whilst in 2012 a T1 plus T2 application at the mid and late timings gave the largest increases. Fungicide treatment increased ($P<0.001$) MGW in all site-years. At ADAS 2011 applications at T1 gave a 5% increase in MGW over untreated crops; there was no further response to a second application at T2. By contrast, at SRUC in both 2011 and 2012, there was a 2-7% increase from the T1 application and a further 2-5% increase from an additional application at T2. The greatest MGW was achieved with the T1 plus mid T2 application (Table 1). There was no significant variety x fungicide interaction for either grains m^{-2} or MGW.

3.2.3 Healthy area light interception

Fig. 4 shows the effectiveness of a given fungicide timing treatment in protecting canopy healthy area PAR interception at different stages during grain filling. Results are expressed as the fraction of incident PAR that is intercepted by healthy tissue. At or shortly after 50% ear emergence (GS 55 to GS 55+1 week) between 0.85 and 0.90 of the incident PAR was intercepted by healthy tissue in crops in each of the site years. In each case, those treated with fungicide at T1 intercepted a 2-5% greater fraction ($P<0.05$) than untreated crops. However, a second application at T2 had no additional effect

at this growth stage at any of the sites and years. A significant benefit of a T2 application in protecting canopy PAR interception was observed from GS 55+2 weeks at SRUC in 2012 where disease was severe and SRUC in 2011 where disease was low to moderate, but only from mid to late grain filling at ADAS (at GS 55+4 weeks). In general a T1 plus late T2 application gave marginally greater protection of fractional healthy area PAR interception compared to T1 plus early and mid T2 timings, but the differences were small and only became apparent in the latter stages of grain filling (later than GS 55+4 weeks) after appreciable canopy senescence had occurred (Fig. 4).

When data from the different site-years of fungicide experiments were combined with those from the shading experiment at SRUC in 2011, there was a strong overall linear relationship ($R^2 = 0.95$) between healthy area PAR interception from GS55 to canopy senescence and grain yield (Fig. 5). The effects of fungicide treatments on healthy area PAR interception and yield were relatively small compared to differences between site-years and the effects of shading. Closer inspection of the results from the ADAS and SRUC 2011 fungicide timing experiments (the two experiments with the highest post-anthesis HAint) show that the relationship between yield and healthy area PAR interception was non-linear (Fig. 6). There was little increase in yield when post-anthesis healthy area PAR interception was increased above ~200 MJ m^{-2} at SRUC and ~290 MJ m^{-2} at ADAS. Split-line regression gave breakpoints of 204 ± 1.8 (± SE) and 293 ± 2.6 respectively. These relationships were generated by the fungicide timing treatments. Thus, the T1 fungicide application increased healthy area PAR interception and yield relative to untreated plants at each site. The T2 applications, on the other hand, increased healthy area PAR interception still further, but had little effect on yield. There was a linear relationship between post-anthesis healthy area PAR interception and yield (averaged across varieties) at SRUC 2012 ($P<0.01$, $R^2 = 0.93$; data not shown).

3.3 Response of yield to post-anthesis shading

When plots were shaded from GS55 through to harvest, there was a large ($P<0.001$) reduction in yield compared to non-shaded plots (Fig. 7). The reduction ranged from 19 to 77% depending on the site-

year. As the shading was imposed progressively later during the grain filling period, its effects on yield diminished until there was no discernible effect. The overall pattern of response was similar at each of the site-years although the magnitude of the effect on yield differed. A split-line regression was fitted to the relationship at each site and the breakpoint taken to be the duration of protection of canopy PAR interception required to maximise yield (Fig. 7). The duration ranged from 3.0 weeks at SRUC 2010 to 5.4 weeks at SRUC 2011 (Table 2) equating to 271-479 ^{o}Cd from GS55 across sites and years. Maximum ear dry weight (the end of grain filling) of unshaded crops was attained around 576 to 711 ^{o}Cd after GS55 depending on the site and year (Table 2). Linear interpolation between measured values of ear growth in unshaded plots was used to estimate the ear dry weight at the end of the period required for canopy protection (in ^{o}Cd) and results expressed as a percentage of the maximum ear weight (Table 2). Thus, canopy protection was required until 72 to 90% of the final ear weight (and by analogy grain weight) had been attained.

Shading had negligible effects on meteorological conditions other than the reduction in incident PAR. On average mean air temperature was just 0.1^{o}C and relative humidity 1.5-2.0% greater under shade compared to unshaded plots. Shading had no significant effect on the gravimetric soil moisture content measured at any depth of the soil profile at the end of grain filling.

4. Discussion

Our results show that PAR interception by spring barley does not need to be protected for the entire duration of grain filling in order to maximise grain yield. Shading experiments on largely disease-free crops suggests that canopy PAR interception must be protected until approximately 80% of grain filling (averaged across sites) has been completed. At this time there can still be 25-45% green leaf area remaining in healthy crops, but the remaining healthy area duration is not contributing substantially to yield.

Yield of barley is generally considered to be sink-limited, especially in the cool temperate climate of NW Europe (Bingham et al., 2007; Kennedy et al., 2017; but see Alvarez Prado et al., 2013 for

evidence of source limitation in contrasting environments). In sink-limited crops, the availability of assimilates for grain filling exceeds the grain storage capacity. Assimilates may be derived from post-anthesis photosynthetic activity and from the mobilisation and re-translocation of pre-anthesis storage reserves (Grashoff and d'Antuono 1997; Bingham et al. 2007). When photosynthetic activity is restricted through disease, or shading as a proxy for disease, sink-limited crops may be able to complete grain filling without a loss of yield by a combination of post-anthesis assimilation and translocation of storage reserves accumulated pre-anthesis. In some circumstances, a higher proportion of reserves may be translocated if there is a greater shortfall in post-anthesis assimilation (Bingham et al, 2009).

Using values for the fraction of grain filling that is insensitive to reductions in post-anthesis PAR interception and the unshaded yield, it is possible to estimate the quantity of grain dry matter that would need to be derived from storage reserves if shading reduced the rate of net canopy photosynthesis to zero. The quantity ranged from 0.54 to 1.25 t ha^{-1}, which is within the range reported for the stem water soluble carbohydrate reserves of barley crops (Bingham et al., 2007; Bingham et al., 2012; Kennedy et al., 2017). Thus, the completion of grain filling from storage reserves could explain the insensitivity of yield to late shading. However, even under relatively dull conditions (e.g. 400 µmol m^{-2} s^{-1} PAR), irradiance on the upper leaves of the canopy under shades would be above the light compensation point for photosynthesis. Shading might also result in an increase in radiation use efficiency (Kennedy et al., 2018). Thus, some net canopy photosynthesis is to be expected in shaded crops so the quantities of stem storage reserves required to sustain grain filling during late shading are likely to be overestimated.

The observed variation between experiments in the duration of protection required (expressed in terms of the progress of grain filling, i.e. 72-90%) may arise from variation in the source-sink balance of the different crops. Crops with a large potential supply of assimilate relative to their grain sink capacity would be expected to require canopy protection for a shorter fraction of the grain filling period than crops whose source and sink are in closer balance. Considerable variation in source-sink

balance has been reported for winter barley crops across sites and years and this was associated with variation in the utilization of stem storage reserves (Bingham et al., 2007). Similarly, reserve remobilisation by healthy wheat crops ranged from 20 to 75% between seasons (Serrago and Miralles, 2014) again suggesting seasonal variation in source-sink balance. Differences in the rate of crop development between sites and years, in addition to the variation in source-sink balance, will contribute to the variation observed in duration of protection required when expressed on a calendar rather than fraction of grain filling basis.

Fungicide applications to wheat and barley crops between flag leaf and ear emergence are widely used to prolong photosynthetic activity during grain filling (Dimmock and Gooding, 2002; Pepler et al., 2005; Walters et al., 2012; Serrago and Miralles 2014). The yield increases in response to fungicide treatment have been related to the greater longevity of green canopy area (Gooding et al., 2000; Pepler et al., 2005; Serrago et al., 2009). Increased green area duration may result, not only from a reduction in visible disease symptoms and hence a smaller loss of healthy tissue, but also potentially the control of phyllosphere saprophytes (Smedgard- Petersen and Tolstrup, 1985; Bertelsen et al., 2001) or direct physiological effects on the rate of leaf senescence (Grossman and Retzlaff, 1997; Wu and von Tiedemann 2001; Cromey et al., 2004; Berdugo et al., 2013). The strobilurin (QoI) and succinate dehydrogenase inhibitor (SDHI) groups of fungicides, and some demythylase inhibitors (DMIs), have been associated with delayed leaf senescence in the absence of visible disease (Zhang et al., 2010). However, the advantages from maximising canopy duration would only be expected if crop yield was source-limited. Once the assimilate supply has been maintained sufficiently to meet the grain storage capacity, further increases in yield will cease. Thus, even in wheat crops grown in light-limited environments such as the UK where source limitation may occur (Beed et al., 2007), there is evidence of an upper limit to canopy duration. Pepler et al. (2005) reported that extending flag leaf lifespan to greater than 700 or 725°Cd (depending on the year) after anthesis by the use of fungicide had no additional effect on yield.

Our results with spring barley show that application of fungicides made after flowering can prolong healthy area PAR interception later into the season than treatments made earlier. Thus, application at GS71 (late T2) resulted in a greater PAR interception than if the application was made at GS37 (early T2) or GS51/53 (mid T2). However, the differences between T2 timings only became apparent during the latter stages of grain filling, typically five or more weeks after flowering. This is beyond the critical period requiring protection identified from shading experiments. Not surprisingly, therefore, varying the timing of T2 applications had little effect on yield when disease severity was low to moderate, giving rise to a non-linear relationship between healthy area PAR interception and yield at these sites (ADAS 2011 and SRUC 2011). In fact here, a T1 application on its own gave sufficient canopy protection during the critical early to mid-grain filling stages to maximise yield. Where disease was severe (SRUC 2012), a T1 on its own was not sufficient to protect fractional PAR interception during early to mid-grain filling or maximise yield. An additional T2 application just prior to ear emergence was required. This increased the fraction of PAR intercepted by healthy tissue, at first (GS55 plus 2 weeks) relative to the T1 only treatment and later (GS55 plus 4 weeks) to the T1 plus early T2 treatment as well. However, even at this site, where disease severity was high, there was no yield benefit from a late fungicide application (i.e. after flowering) compared to earlier timings. The small improvements observed in fractional healthy area PAR interception appeared to occur too late to significantly affect total cumulative PAR interception and grain filling.

Some caution must be exercised when comparing results from the shading and fungicide timing experiments because, by necessity, different varieties were used in each and the experiments spanned a different range of years. Further, the ability of crops to adjust radiation use efficiency or biomass partitioning in response to shading and disease-induced reductions in PAR interception may differ. Nevertheless, both sets of experiments have demonstrated that, across a range of varieties and site-years, yield is insensitive to changes in PAR interception by healthy canopy during the latter stages of grain filling.

The above findings are consistent with fungicide treated spring barley crops being sink-limited. It is noteworthy too that crops that differed widely in yield behaved in a similar way to fungicide timing when disease severity was comparable. It might be expected that grain filling in crops with a large grain number (sink capacity) would be less sink-limited (i.e. source- limited or tending towards source-limitation) and thereby more responsive to delaying canopy senescence with fungicide than crops with a small grain number. However, there was no evidence from the current study to support this. The greater yields at ADAS compared to SRUC in 2011 were associated with an 18% larger grain number (15,590 compared to 13,199 respectively), but in each case the relationship between healthy area PAR interception and yield was non-linear. This suggests an appreciable and comparable sink-limitation at each site. In order for a crop to have a larger sink capacity than another, but its yield still remain sink-limited, it must also have a larger source of assimilate for grain filling. At ADAS the larger source was, for the most part, the result of the greater incident PAR during grain filling (31%; 522 *cf* 399 MJ m^{-2} PAR for ADAS and SRUC 2011 respectively) rather than substantive differences in fractional healthy area PAR interception (0.58 and 0.54 respectively averaged over the grain filling period). Differences in radiation use efficiency and utilisation of stem storage reserves may be expected between sites. However increases, if any, are unlikely to account for much of the additional assimilate needed for grain filling at ADAS given the relative scale of differences observed in incident PAR.

In this paper we have focussed on the effects of protecting canopy PAR interception during grain filling on yield formation. Decisions regarding disease management and fungicide use must also consider likely effects on grain quality. An important quality characteristic for malting barley crops is grain N%, which can vary according to starch deposition (the dilution effect) as well as N accumulation in the grain. Effects of disease control by fungicide on grain N concentration depends on the pathogen in question. Control of biotrophs such as rusts and mildews of cereals can increase grain N concentrations, whilst N concentrations following the control of necrotrophic or hemi-biotrophic pathogens tend to be maintained or reduced compared with untreated crops (Conry and Dunne, 2001; Dimmock and Gooding 2002; Ruske et al., 2003;). Changes in N% are generally small after controlling

necrotrophs and hemi-biotrophs because fungicides increase post-anthesis N uptake from soil and the efficiency of N remobilisation from vegetative organs to the grain in addition to increasing grain yield (Ruske et al., 2003). The major pathogens of barley production systems in NW Europe are necrotrophs or hemi-biotrophs (e.g. *R commune* and *R collo-cygni*). Thus we argue that strategies designed to rationalise fungicide use whilst maximising yield should be compatible with achieving target grain N% specifications.

5. Conclusions

The results indicate that canopy PAR interception does not need to be protected for the entire grain filling period in order to maximise yield of spring barley. Yield was insensitive to large scale reductions in PAR imposed by shading once 72-90% of eventual grain dry matter had been deposited. Fungicides applied before flowering provided sufficient protection of PAR interception during grain filling to maximise yield irrespective of the severity of disease. Later applications increased canopy duration and PAR interception by healthy tissue during grain filling, but these effects occurred beyond the critical period requiring protection and so did not increase yield. The results provide a mechanistic understanding on which to base fungicide decisions. Although different fungicide active ingredients were not compared in the present work, there would appear to be no justification for selecting treatments simply to maximise post-anthesis canopy lifespan. Decisions should be based on considerations of the disease risk and the efficacy of disease control to ensure protection of canopy PAR interception during the critical early to mid-stages of grain filling. The optimum timing of fungicide does not appear to vary with the yield potential of the site, but does vary with the disease severity.

Acknowledgements

We thank the technical staff of SRUC and ADAS for conducting the experiments, and AHDB, Defra and the Scottish Government for funding. The contributions of Steve Waterhouse (BASF), Andrew Flind (Bayer), James Southgate (Agrii) and Paul Beech (Agrii) are gratefully acknowledged. SRUC receives

financial support from the Scottish Government's Rural Environment Science and Analytical Services (RESAS) division.

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Table 1. Grain yield and yield components in response to different fungicide timing combinations. Yield and mean grain weight (MGW) are expressed at 100% dry matter content. Timings were: T1, GS30/31; T2 early, GS37; T2 mid, GS49/55; T2 late, GS71. Data were analysed by two way ANOVA. LSD values are for P=0.05.

	ADAS 2011				SRUC 2011				SRUC 2012			
Fungicide	Forensic	Optic	Waggon	Mean	Forensic	Optic	Waggon	Mean	Forensic	Optic	Waggon	Mean
Yield t ha^{-1}												
Untreated	6.89	6.38	6.21	6.49	5.12	5.55	6.11	5.59	2.88	3.00	3.57	3.15
T1 only	7.22	7.36	6.94	7.17	5.75	5.98	6.09	5.94	3.27	3.44	3.74	3.48
T1 + T2 early	7.14	7.52	6.58	7.08	5.97	6.02	6.20	6.06	3.37	3.49	3.88	3.58
T1 + T2 mid	7.35	7.42	6.87	7.21	5.96	6.01	6.15	6.04	3.49	3.65	4.04	3.73
T1 + T2 late	7.30	7.68	6.72	7.23	5.98	6.15	6.12	6.08	3.46	3.61	4.14	3.74
	df	p	lsd		df	p	lsd		df	p	lsd	
Variety (V)	6	0.002	0.240		6	0.046	0.285		6	0.012	0.327	
Fungicide (F)	35	<0.001	0.282		36	<0.001	0.200		36	<0.001	0.109	
V*F	40.8	0.177	0.477		29.4	0.041	0.389		11.29	0.544	0.346	
same level of V	35		0.488		36		0.343		36		0.189	
Grains m^{-2}												
Untreated	15263	14285	14967	14838	11864	13264	12667	12598	8339	9314	9737	9130
T1 only	15272	15530	15914	15572	12809	14379	12309	13166	9113	9547	9625	9428
T1 + T2 early	15006	16156	15337	15500	13294	13918	12676	13296	8962	9379	9850	9397
T1 + T2 mid	15542	15078	15803	15475	12938	13817	12399	13052	9105	9719	10091	9638
T1 + T2 late	15243	16267	15546	15685	13044	14506	12293	13281	9164	9569	10407	9713
	df	p	lsd		df	p	lsd		df	p	lsd	
Variety (V)	6	0.505	519.0		6	0.004	676.3		6	0.044	744.1	
Fungicide (F)	35	0.120	678.1		36	0.025	461.9		36	0.004	306.8	
V*F	41	0.179	1129.4		28.8	0.056	917.0		14.4	0.320	821.4	
same level of V	35		1174.5		36		800.1		36		531.5	
MGW, mg												
Untreated	45.20	44.77	41.60	43.86	43.10	41.85	48.19	44.38	34.60	32.27	36.70	34.53
T1 only	47.27	47.35	43.65	46.09	44.88	41.61	49.45	45.32	35.92	36.04	38.81	36.92
T1 + T2 early	47.60	46.75	42.91	45.75	44.85	43.27	48.85	45.66	37.65	37.19	39.36	38.06
T1 + T2 mid	47.36	48.58	43.50	46.48	46.05	43.45	49.59	46.36	38.32	37.60	40.00	38.64
T1 + T2 late	47.92	47.21	43.24	46.13	45.77	42.38	49.77	45.97	37.79	37.71	39.75	38.42
	df	p	lsd		df	p	lsd		df	p	lsd	
Variety (V)	6	<0.001	0.998		6	<0.001	0.882		6	<0.001	0.722	
Fungicide (F)	36	<0.001	0.927		36	<0.001	0.788		36	<0.001	0.793	
V*F	38.4	0.607	1.654		37.5	0.161	1.421		41.2	0.174	1.361	
same level of V	36		1.605		36		1.365		36		1.374	

Table 2. The duration of protection of canopy PAR interception required to maximise yield determined from post-anthesis shading treatments in three site-years. The duration is expressed in calendar weeks or ^{o}Cd after 50% ear emergence (Zadoks GS55) and as the % of grain filled (the % of final grain weight at the time when there was no subsequent response to shading). The duration of grain filling and final yield of unshaded plots is given for reference. Values were determined from data in Fig 7.

	Duration of protection			Duration of grain fill	
Site	Weeks after GS 55	^{o}Cd after GS 55	% of grain filled	^{o}Cd after GS 55	Unshaded final yield, t ha^{-1} @ 100% DM
ADAS 2009	4.5	479	90	576	5.4
SRUC 2010	3.0	271	72	676	4.3
SRUC 2011	5.4	453	78	711	5.7

Figure legends

Fig. 1. Diagrammatic representation of timing of shading treatments. Shades were erected at weekly intervals commencing at ear emergence (GS55) and once erected left in place until harvest. Onset and duration of shading is illustrated by the horizontal lines representing the six shading treatments. Control plots were left unshaded throughout.

Fig. 2. Average daily temperature and accumulated monthly rainfall for experimental sites and years. Bars are the season specific values and broken lines the 30 year long-term average (1981-2010). As some rainfall data for the ADAS site were missing, the data presented are from a UK Met Office station 30 km from the experimental site. Thus, they represent weather patterns for the region rather than site specific data.

Fig. 3. Severity of disease or disorder (spotting) of untreated plots averaged over the top three leaves during grain filling (GS73-83). Data were arcsine transformed for ANOVA; values are back-transformed means. For a particular disease or disorder, varieties with a different letter are significantly different at $P<0.005$. Note the different scale used for SRUC 2012. Abreviations are: Mil, powdery mildew; Ram, ramularia leaf spot; Rhynch, rhynchosporium leaf scald; Spot; physiological brown spotting.

Fig. 4. PAR interception by healthy leaf area expressed as a fraction of the daily incident radiation at different stages during grain filling (weeks after GS55) and with different fungicide timings. Columns represent means for the different fungicide timings across three varieties; untr is the untreated control. For a particular time after ear emergence, the

number above the columns is the LSD $_{0.05}$ for the main effect of fungicide treatment; columns with a different letter are significantly different at P<0.05.

Fig. 5. Relationship between grain yield and post-anthesis PAR interception by healthy area. Data are from the post-anthesis shading experiment on variety Westminster (SRUC 2011) and fungicide timing experiments at ADAS and SRUC. Individual plot values are shown for the shading experiment SRUC 2011. Values for fungicide timing treatments at SRUC 2012 and ADAS 2011 are means across three varieties and four replicate plots; at SRUC 2011 values are for individual varieties averaged across four replicate plots. Line fitted by linear regression to all data.

Fig. 6. Non-linear relationships between post-anthesis healthy area PAR interception and yield arising from fungicide timing treatments at sites with low to moderate disease severity. At ADAS 2011 there was no significant interaction between cultivar and fungicide timing on yield and hence mean values across three varieties and four replicate plots are presented. At SRUC 2011 values are means of individual varieties across four replicate plots.

Fig. 7. Relationship between grain yield and the time at which post-anthesis shading was imposed (solid line and closed symbols). Shades were erected at weekly intervals starting at 50% ear emergence and left in place until harvest. Each point represents an individual replicate plot. Lines fitted by spilt-line regression. Open symbols and broken lines show the % green leaf area (GLA) averaged over the top four leaves of unshaded control plots. Values are the means of three replicate plots. Error bars are omitted for clarity.

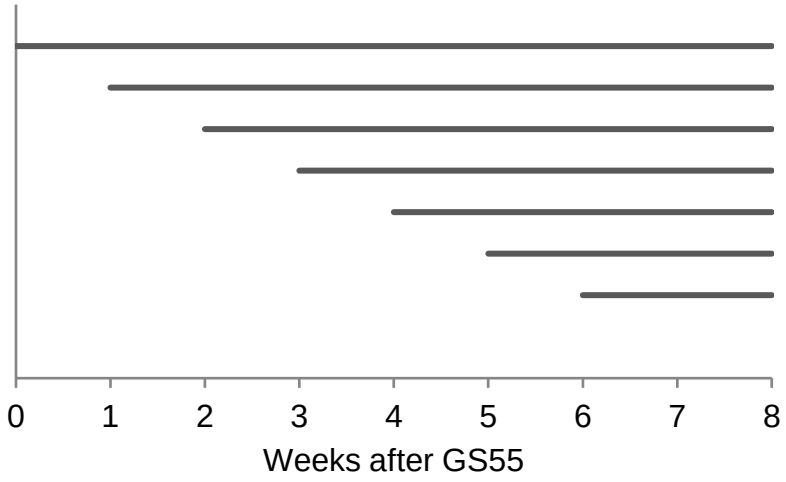


Figure 1

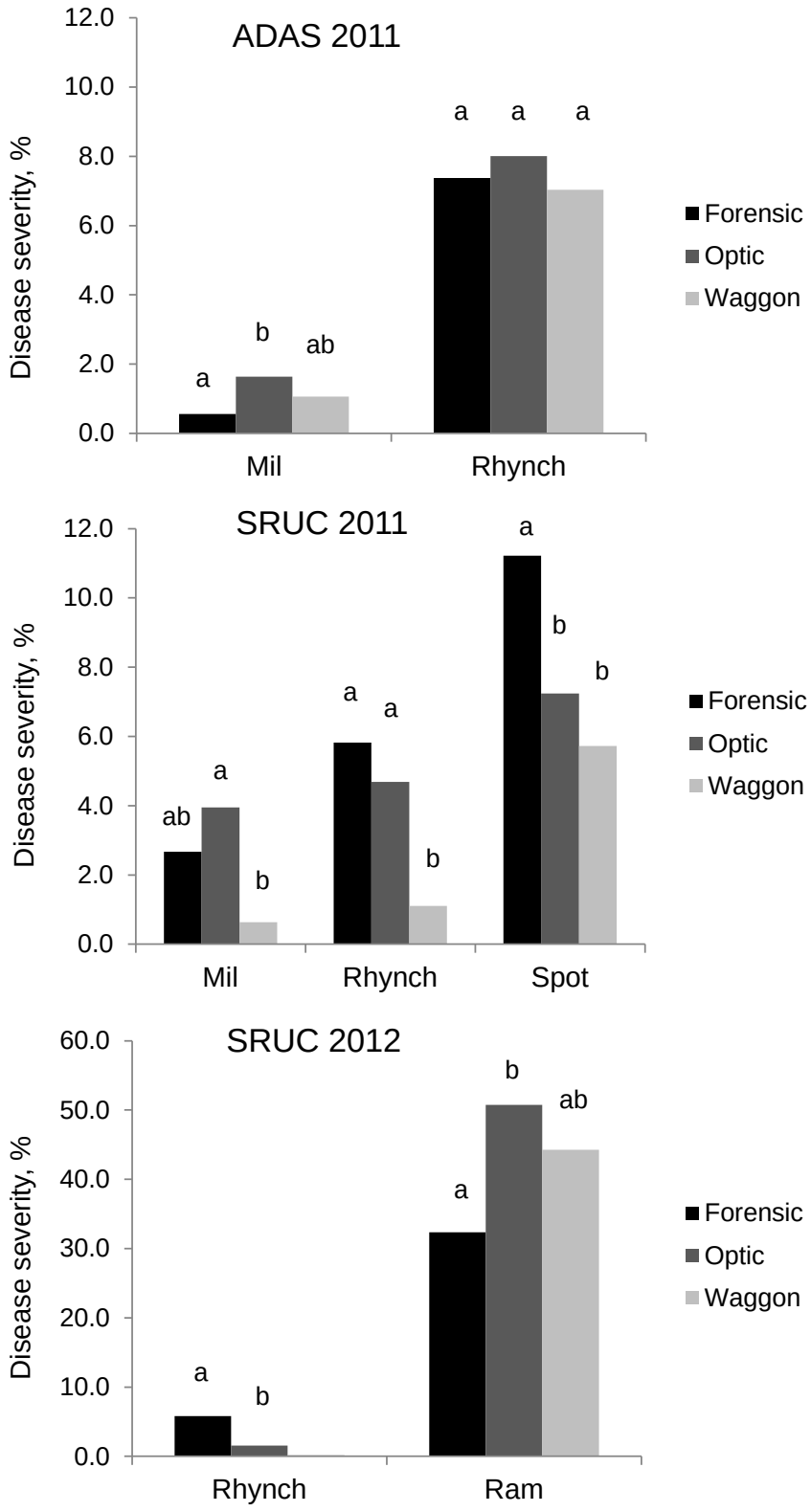

ADAS 2011
Disease severity, %
12.0
10.0
8.0
6.0
4.0
2.0
0.0
a
b
ab
a a a
Mil
Rhynch
Forensic
Optic
Waggon
SRUC 2011
Disease severity, %
ab a b
a a b
a b b
Mil
Rhynch
Spot
Forensic
Optic
Waggon
SRUC 2012
Disease severity, %
60.0
50.0
40.0
30.0
20.0
10.0
0.0
a b
a b ab
Rhynch
Ram
Forensic
Optic
Waggon

Figure 3

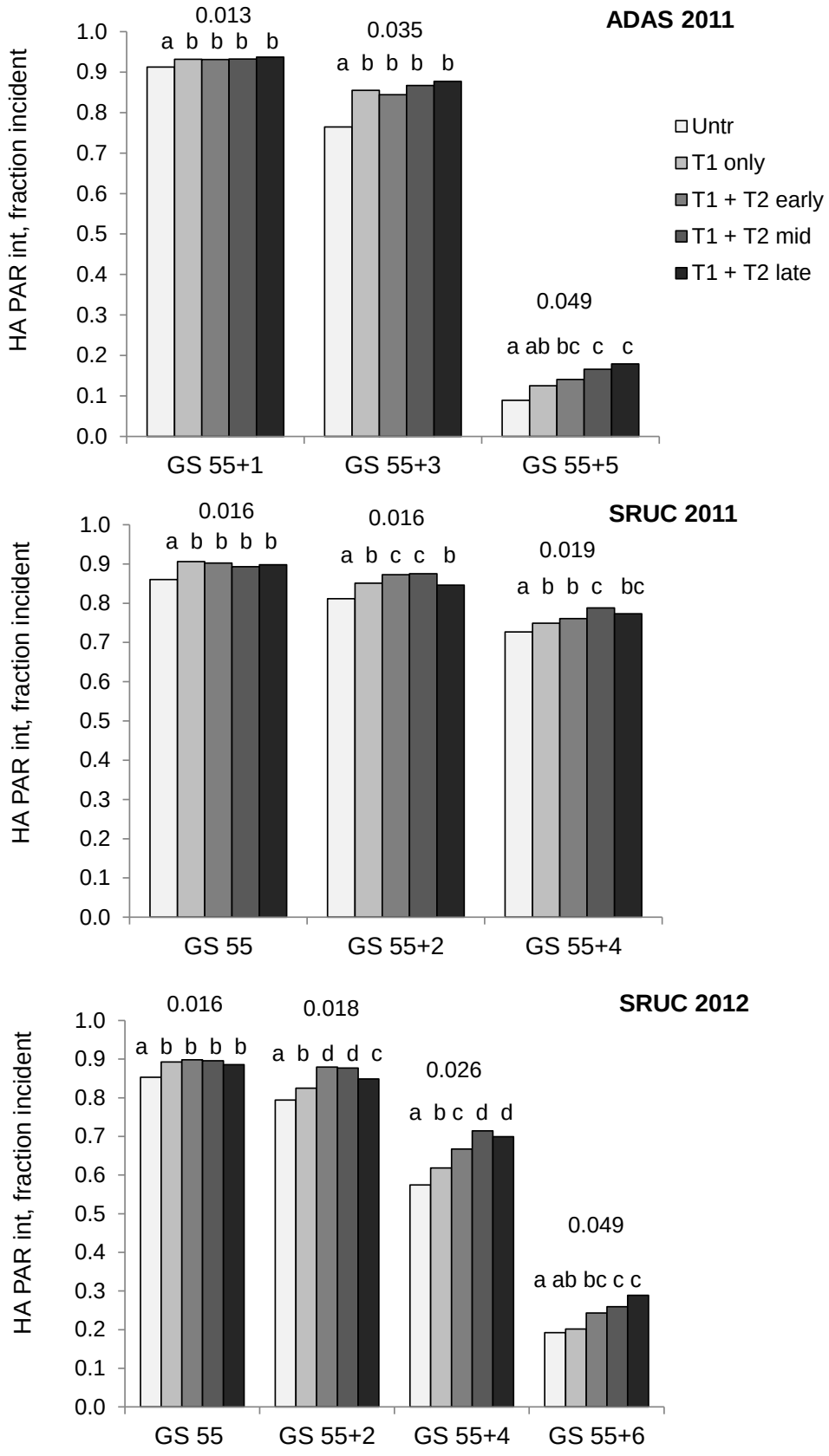

ADAS 2011
HA PAR int, fraction incident
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.013
a b b b b
0.035
a b b b b
0.049
a ab bc c c
GS 55+1
GS 55+3
GS 55+5
Untr
T1 only
T1 + T2 early
T1 + T2 mid
T1 + T2 late
SRUC 2011
HA PAR int, fraction incident
0.016
a b b b b
0.016
a b c c b
0.019
a b b c bc
GS 55
GS 55+2
GS 55+4
SRUC 2012
HA PAR int, fraction incident
0.016
a b b b b
0.018
a b d d c
0.026
a b c d d
0.049
a ab bc c c
GS 55
GS 55+2
GS 55+4
GS 55+6

Figure 4

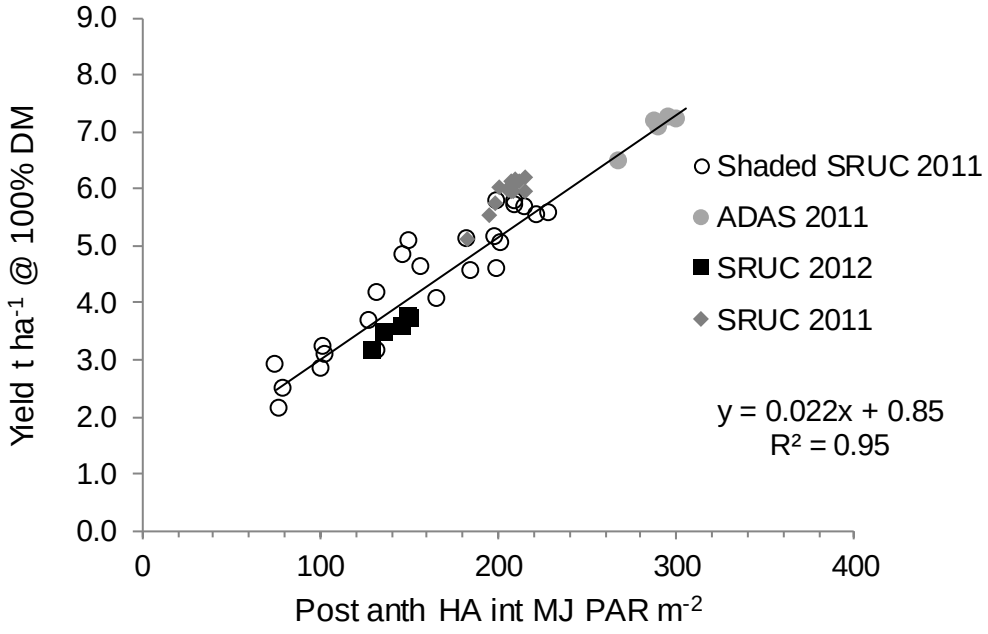
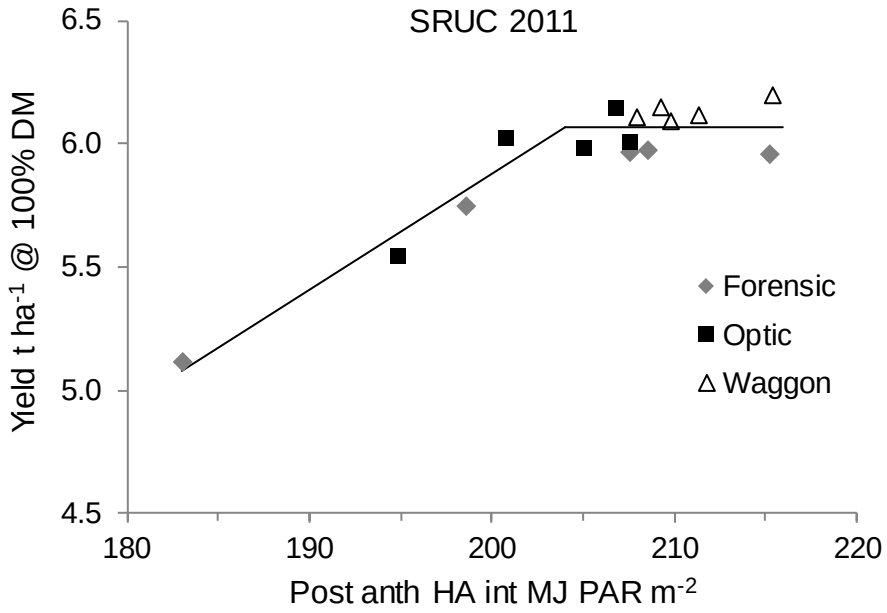

9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0
100
200
300
400
Yield t ha-1 @ 100% DM
Post anth HA int MJ PAR m-2
Shaded SRUC 2011
ADAS 2011
SRUC 2012
SRUC 2011
y = 0.022x + 0.85
R² = 0.95

Figure 5


SRUC 2011
Yield t ha-1 @ 100% DM
6.5
6.0
5.5
5.0
4.5
180
190
200
210
220
Post anth HA int MJ PAR m-2
Forensic
Optic
Waggon

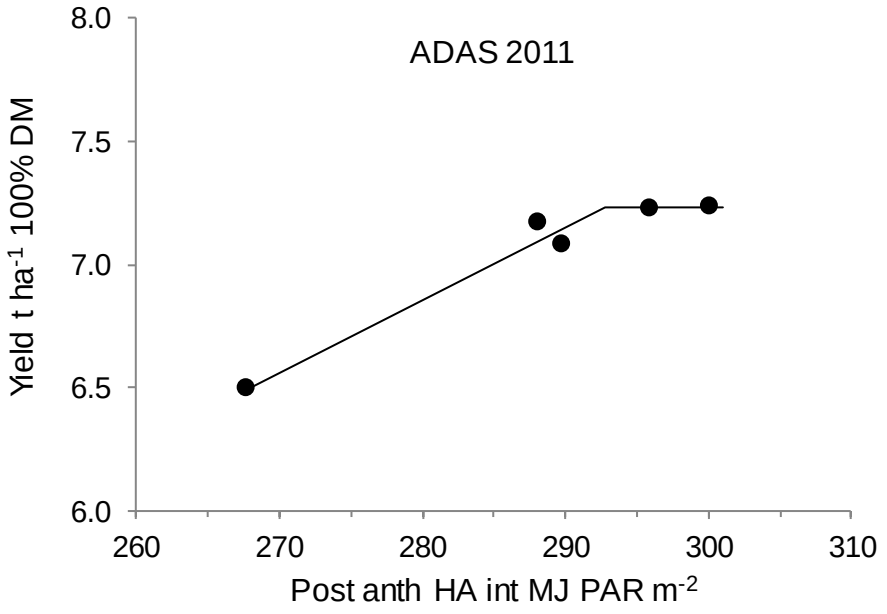

ADAS 2011
Yield t ha-1 100% DM
8.0
7.5
7.0
6.5
6.0
260
270
280
290
300
310
Post anth HA int MJ PAR m-2

Figure 6

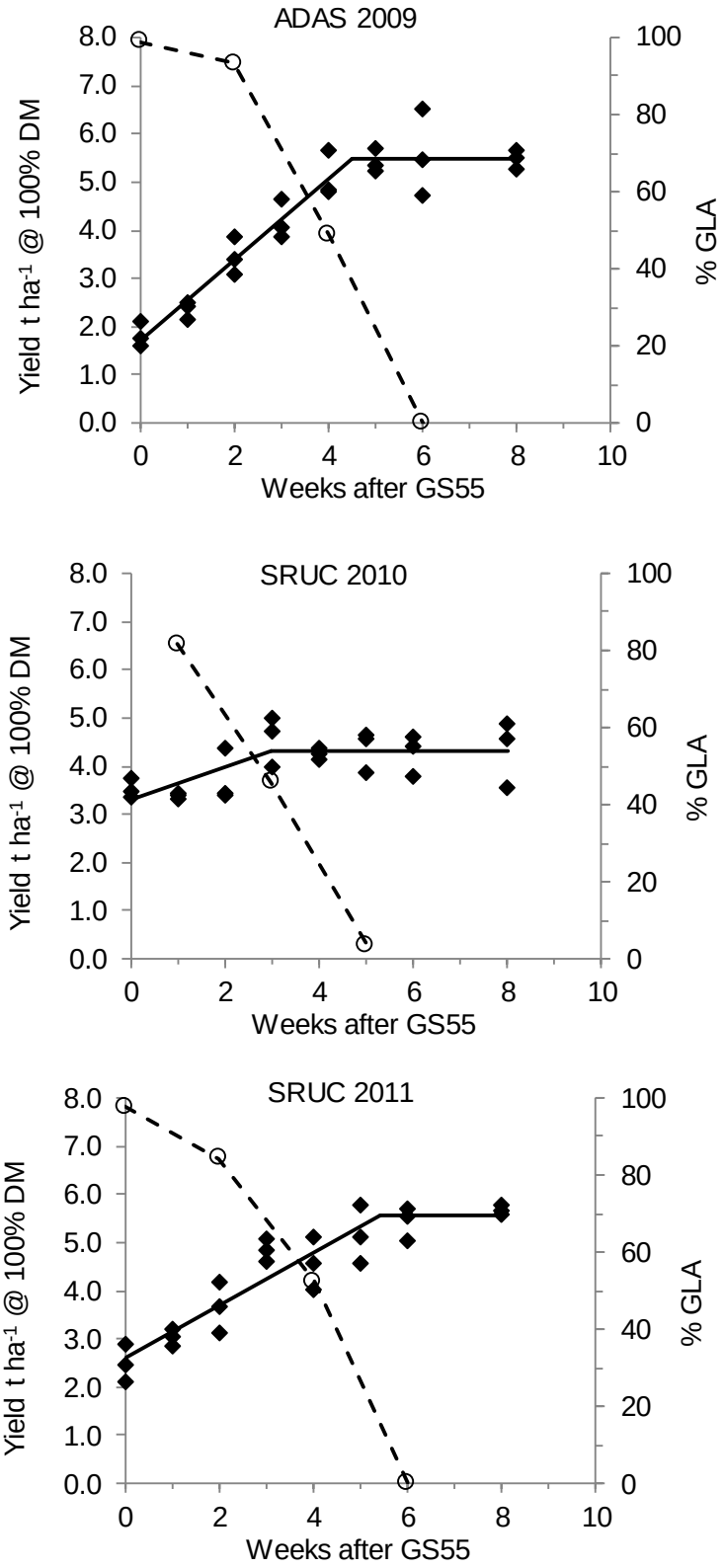

ADAS 2009
SRUC 2010
SRUC 2011
Yield t ha-1 @ 100% DM
% GLA
Weeks after GS55
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
0
20
40
60
80
100
0
2
4
6
8
10

Figure 7