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Understanding the control of yield formation in two- and six-row winter barley varieties to target disease management

Robert Beattie

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I would like the dedicate this thesis to the memory of

Dr. John Finnan

Contents

Declaration

I hereby declare that this thesis has been composed by me and that the work presented herein is my own, unless otherwise stated. This work has not been submitted for any other degree or professional qualification.

Robert Beattie

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Lay Summary

In a climate such as Ireland, the use of fungicides to control crop disease is vital to maximise yield, but for production to be economically and environmentally sustainable their use must be targeted at those periods of the crop's life that are most sensitive to disease. Hybrid six-row winter barley varieties are becoming increasingly popular with growers. Six-row varieties have six rows of grains along each ear, whereas two-row varieties have just two. The six–row varieties, therefore, produce more grains per unit area of land, but the average weight of each grain is lower. It is recognised that the overall yield of two-row varieties is usually limited by the number of grains they produce and their storage capacity. These crops produce more than enough material in photosynthesis to fill the grains. This is known as 'sink' limitation of yield. It has been suggested that because six-row varieties produce a large number of grains, their yield might be limited by their ability to provide material to fill them (this is known as 'source' limitation). The leaves of six row varieties might, therefore, need greater protection from disease after flowering when the grains are filling than two-row varieties. The objectives of this project were firstly to test whether a six-row variety needs later fungicide applications than a two- row variety to maximise yield and secondly to investigate whether the limitations to yield in a six-row barley variety are different to those of a two row variety.

Field experiments were carried out from 2015 to 2018 to determine if current fungicide timing needed to be altered based on row-type. Fungicides were applied as part of programmes ranging from no application of fungicide to programmes with 4 applications during the growing season. The results showed that despite the larger number of grains per unit area in the six-row variety that the response to fungicide was similar in both row-types. The timings that had the greatest benefit to yield were when the stem begins to elongate and as the awns were emerging. A further experiment was carried out to investigate whether yield in a six-row variety is limited by 'sink' or 'source'. The results showed that both row-types produced more than enough material to fill the grains i.e. yield was sink-limited.

The results so far indicted that the lower average grain weight in a six-row variety is not caused by a lack of material to fill the grains, therefore the storage capacity of these grains must be lower than of that of a two-row variety. Previous research indicated that grain storage capacity and the number of grains per unit area may be determined at the same time.

To investigate this, the effects of varying light availability in both row-types was investigated during the period where the number of grains is determined. Varying light availability changed ear growth during the treatment period, although these effects did not translate into effects on grain weight or the number of grains per ear at harvest. It is clear that further work is required to better understand what controls the storage capacity of grains in barley. If better understood, yield could be increased as there is an excess of material to fill the grains.

The results of this research show that disease management strategies designed for two-row winter barley are also suitable for six-row varieties because yield in both is limited by the number and storage capacity of the grains produced.

Abstract

To improve the sustainability of cereal production, fungicides should only be applied to crops where they are likely to result in an economic increase in yield or grain quality. In recent times, there has been increased utilisation by growers of hybrid six-row barley varieties due to their high yields in recommended list trials in both the UK and Ireland. Six- and two-row winter barley differ in their yield components, with studies showing that six-row types produce fewer ears m^{-2} and more grains ear^{-1} (leading to an overall higher number of grains m^{-2}), but a lower average (mean) grain weight when compared with two-row varieties. It was hypothesised that a six-row variety would require a different approach to the management of disease compared to a two-row. Six-rows might require greater protection post-anthesis to maximise assimilate supply for grain filling whereas current barley recommendations, developed for two-rows, emphasise protection pre-flowering to maximise the development of grain sink capacity. This is because yield formation in six row varieties, with their larger number of grains may be more source-limited (limited by the supply of assimilates) than in two-row varieties where yield is generally considered to be sink-limited (limited by the number and storage capacity of grains). The main objectives of this project were to 1) compare the responses of a two-row and a six-row winter barley variety to fungicide programmes with different timings of application; 2) determine the source-sink balance of a two-row and six-row barley variety grown with and without fungicide treatment and 3) determine the relative sensitivity of grain sink capacity to variations in pre-anthesis assimilate supply during ear development in both two- and six-row varieties.

To investigate if the disease management strategy needs to be modified according to row-type a field experiment to investigate the yield response to fungicide application timing in a conventional two- (cv KWS Tower) and hybrid six-row (cv Volume) winter barley variety was carried out over three years (2014/2015, 2015/2016 and 2016/2017) at two sites, SRUC, Edinburgh, Scotland and Teagasc, Oak Park Carlow, Ireland. The fungicide applications were applied as part of programmes, ranging from untreated to a four spray programme. The results showed that despite the markedly different yield components of each variety there was no significant interaction between variety and fungicide application ($p>0.05$) suggesting that disease management does not need to be tailored to ear type. Surprisingly there was a

significant yield response to fungicide application at ear emergence, which had not been seen in barley previously. It was hypothesised that either this response resulted from a failure to effectively control ramularia at GS49 or that the response was unique to the two varieties selected for the current study. To test these hypotheses, a further field experiment was carried out at two sites in 2018. Two additional varieties were included to those used previously, a conventional two- (cv KWS Cassia) and six-row variety (cv KWS Kosmos). Fungicide treatments focused on late-season disease control. The results again indicated that there was no difference ($p>0.05$) in how yield of the contrasting ear types responded to fungicide treatment. When ramularia was effectively controlled at GS49, there was no requirement for a later fungicide treatment at ear emergence.

To investigate the source-sink balance during grain filling of cv KWS Tower and cv Volume, a field experiment was carried out at Teagasc, Oak Park in 2016 and 2017. The relative source-sink balance was determined in two ways; firstly by growth analysis and measurement of radiation interception, radiation use efficiency and utilisation of soluble carbohydrate reserves, and secondly by manipulation treatments to alter the assimilate supply per unit grain number 14 days after flowering by row opening, de-graining, and shading. The results indicated that despite the higher grain numbers and smaller MGW in the six-row variety Volume, the source-sink balance in fungicide treated and untreated crops were similar to that of the two-row variety Tower. For both ear types, when disease was allowed to develop in untreated crops, the sink capacity (grain number and potential grain weight) was reduced as well as the source capacity, such that the crops remained sink-limited during grain filling.

The results from the above experiment indicated that the lower grain weight in the six-row variety was not the result of source limitation of grain filling associated with its higher grain number, but rather a smaller potential grain weight. This raises an important question as to the control of grain sink capacity (grain number and potential grain weight). Previous research suggests that the components of sink capacity may be determined pre-anthesis. Thus, the sensitivity of sink capacity to pre-anthesis assimilate supply was tested in both Tower, and Volume in a field experiment carried out in Teagasc, Oak Park in 2017 and 2018. Pre-anthesis assimilate supply was manipulated through shading and row-opening, with investigations of the effects of these treatments on sink capacity carried out on tagged main stems. The results showed that manipulations significantly affected pre-anthesis growth

conditions with shoot growth rate and carpel weight being increased ($p<0.05$) in both varieties when rows were opened and decreased when shaded. However, these changes in pre-anthesis growth conditions and carpel weight did not translate into effects on either MGW or grains ear^{-1}. The results of this study raise important questions about the control of potential grain weight, as the previously held view of a direct relationship between MGW and carpel weight at anthesis is not supported. It is clear that further work into the mechanisms controlling potential grain weight in barley is required. If better understood, yield potential could be raised.

The results of this research show that disease management strategies designed for two-row winter barley are also suitable for six-row varieties because the source-sink balance of the two variety types is comparable. The greatest yield response to fungicide application comes from applications made at the start of stem extension and during booting. There may be opportunities for omitting earlier applications during tiller production depending on the severity and type of the disease present in the crop.

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List of Abbreviations

ANOVA	analysis of variance
WSC	water-soluble carbohydrates
GS	growth (developmental) stage
RO	row-open
KIL	Kildalton experimental site
PAR	photosynthetically active radiation
OP	Oak Park experimental site
S & N rate	Seed and nitrogen rate
SRUC	Scotland's Rural College and experimental site
RUE	radiation use efficiency
PGW	potential grain weight
HI	harvest index
F1	first generation
mm	millimetre
MJ m^{-2}	megajoules per metre squared
t ha^{-1}	tonnes per hectare
g l^{-1}	grams per litre
°C	Degrees Celsius
kg l^{-1}	kilogram per litre
l ha^{-1}	litres per hectare

General Introduction

Barley (*Hordeum vulgare L.)* is one of the founder crops of old-world Neolithic agriculture (Badr et al., 2000, Zohary et al., 2012). The domestication of wild barley is said to have taken place approximately 10,000 years ago (Badr et al., 2000, Fischbeck, 2002). When plants are domesticated, some plants become entirely dependent on humans as they can no longer propagate themselves (Doebley et al., 2006). There have been a series of genetic changes between wild to domesticated plants, with domesticated plants typically have larger grains, are more robust, have increased apical dominance, display synchronised flowering, and the loss of natural seed dispersal allowing the grain to be harvested (Doebley et al., 2006, Gross and Olsen, 2010). The location of the first domestication of barley was in the southern part of the fertile crescent (Badr et al., 2000, Jones et al., 2008) and barley is said to be one of the earliest domesticated crops (Fischbeck, 2002, Zohary et al., 2012).

Barley is an essential crop in human history, and it remains an important crop today. In terms of production quantity, barley is ranked 4th amongst cereal crops in the world after maize, rice and wheat, and 11th overall (Newton et al., 2011). Barley is grown on 50 million hectares worldwide, with production recorded in 104 countries (average 2008 to 2013 (FAO, 2015)). The largest producer in the world is the Russian Federation, with the top three yields coming from the UAE, Belgium, and Ireland, respectively (FAO, 2015). Barley is seen as the most widely adopted cereal grain due to the production of the crop in a wide range of latitudes and is cultivated farther into deserts than other cereal crops (Baik and Ullrich, 2008). The reason for this widespread production of barley is that it can survive in drier conditions, handle poorer soils, and is capable of growth with some salinity when compared with other cereal crops (Zohary et al., 2012).

It is expected that food production will need to increase by 50% by 2050 to meet the demand of an increasing global population (Chakraborty and Newton, 2011). Modern agriculture is faced with reaching this demand and ensuring food security, in the face of challenges such as climate change, policy influences and pesticide resistance. Cereal production has increased two-fold over the last 40 years. During the ‘green revolution', the use of synthetic pesticides to control crop pests effectively played a significant role in this increase (Oerke, 2006). The use of these synthetic pesticides to control crop pests has increased 15-20 fold

during this period, although the portion of crop loss has increased during the same period (Oerke, 2006) indicating that plant pests are evolving to the selection pressure that modern agriculture is placing on them. One of the most important pests of cereal crops are plant fungal pathogens, which are estimated to account for 10-16% of the world's global cereal harvest annually (Oerke, 2006, Strange and Scott, 2005), although they could potentially account for over 50% of yield if left uncontrolled (Oerke, 2006). Thus, it is evident that plant pathogens present a threat to food security in the future.

Cultural methods such as rotation and genetic resistance are utilised to control these pathogens (Hillocks, 2012), although effective control is still reliant on the use of conventional pesticides (Poole and Arnaudin, 2014). These pesticides are only to be used when necessary as part of an integrated pest management (IPM) strategy as governed by the European Union Directive 2009/128/EC.

Barley has been an essential part of human history. In old-world agriculture, the primary use of barley was for human food. In modern times this has been replaced by animal feed and malt production, although with recent trends moving towards the incorporation of more barley-based products into the human diets for health benefits the human consumption of barley is likely to increase (Baik and Ullrich, 2008, Sullivan et al., 2011).

Irish agriculture is a largely grass-based system with cereal production, accounting for 5.9 % (261,000 ha) of the total farm area (Anon., 2018b) 70% of the cereal area is made up of barley (Anon., 2018a). There are several reasons for this percentage being so substantial including, land suitability, demand for straw, malt production and tradition. The majority of the barley area, however, is made up of spring-sown barley (68% in 2018) (Anon., 2018a), although this can fluctuate depending on the season as it is estimated that 59% of the barley area in 2019 is spring-sown.

High yields of winter barley have been recorded in recent times with an average yield of 8.8 t ha^{-1} in 2018 (Anon., 2018a). This high yield has coincided with a dramatic rise in the area covered by winter barley, 19,000 ha of winter barley were planted in 2009 while in 2019 it is estimated that the area has risen to 80,000 ha. This dramatic rise is likely to have been caused by improved agronomy, policy changes and genetic improvement. An example of this genetic improvement has been the introduction of hybrid six-row varieties, these varieties have been outperforming their conventional two-row counterparts in the

recommended list trials both in the UK and Ireland (AHDB, 2018, Anon., 2017). Although they are relatively new to the market, there has been little independent research to support current management practices. At present, the management recommendations for both row-types is similar, although this may not be optimal for six-row varieties. This project aims to utilise physiological data and fungicide timing experiments to assess if the disease management strategy needs to be altered based on row-type. Further to this, more targeted, field experimentations aim to determine the sensitivity of grain sink capacity to changes in assimilate supply during the late stem extension period.

Chapter 1 **Background**

1.1 Yield formation

Crop growth and crop development are two very distinct processes which generally take place simultaneously and can be often confused. Therefore, it is essential to define each of the processes clearly. Crop growth is the increase in plant dry weight, which is the net result of acquisition and loss of resources, while crop development is the sequential production and loss of structural units of the plant (Hay and Porter, 2006). The development of cereals is often divided into three distinct phases; vegetative, reproductive and grain filling phases (Kirby et al., 1984, Slafer et al., 2009). The vegetative phase begins with seedling germination and continues until collar initiation (Kirby et al., 1984, Sreenivasulu and Schnurbusch, 2012). During this phase tiller production occurs, this is an critical plant mechanism as it is associated with the capacity of the crop to intercept solar radiation and is a vital component of the number of ears m^{-2} produced (Garcia del Moral et al., 1984). The typical tillering pattern is a rapid increase in number during the vegetative phase, with maximum tiller number generally being reached around the start of stem extension followed by a period of tiller mortality (Kirby, 1967, Garcia del Moral et al., 1984). However, recent evidence shows that this pattern can be quite variable across sites and years (Kennedy et al., 2016).

The reproductive phase can be divided into two sub-phases, the early reproductive phase, in which spikelet initiation occurs (Kirby et al., 1984, Kernich et al., 1997, Sreenivasulu and Schnurbusch, 2012), and the later reproductive phase where spikelet growth and development takes place (Kirby et al., 1984, Kernich et al., 1997, Sreenivasulu and Schnurbusch, 2012). The initiation phase is where the ear produces its maximum number of spikelet primordia, along with a full complement of floral primordia (Kirby et al., 1984). At this early stage, the maximum number of grains ear^{-1} is already determined (Kirby and Riggs, 1978, Waddington et al., 1983, Kernich et al., 1997). The second sub-phase of the reproductive phase is the spikelet development stage (Kirby et al., 1984, Alqudah and Schnurbusch, 2014). Growth and development of the ear still occur while the ear is enclosed by the sheaths of the flag and second leaves (Kirby et al., 1984). This stage has been

described as the most critical stage for spikelet survival (Alqudah and Schnurbusch, 2014), thus at this stage of development, the final number of grains ear^{-1} is determined.

The plant moves into the final stage (grain filling) with the process of anthesis, which occurs when pollen lands on the stigma (Waddington et al., 1983). Once the plant reaches anthesis, it moves into the grain set and filling phase followed by ripening just before harvest (Slafer et al., 2009). The grain filling phase can be divided into three sub-phases, the first being the lag phase, the second being the dry matter accumulation phase and lastly the ripening/dehydration phase (Smith et al., 1999). The lag phase is a period in which endosperm cell division occurs (Smith et al., 1999). This phase is critical to yield of barley as studies have shown that the endosperm cell number correlates strongly to the final grain weight (Cochrane and Duffus, 1983), with the number of endosperm cells also affecting the rate of dry matter accumulation (Brocklehurst, 1977). The duration of cell division can last up to 30 days post-anthesis (Radley, 1978, Cochrane and Duffus, 1981, Cochrane and Duffus, 1983, Kvaale and Olsen, 1986), although studies have shown that the starchy endosperm storage cells cease growth 12-14 days after anthesis with subsequent cell division being restricted to aleurone cells (Cochrane and Duffus, 1983, Kvaale and Olsen, 1986). Therefore division after 12-14 days post-anthesis will have negligible effects on yield. The next phase is the period of dry matter accumulation. This phase overlaps with the cell division (lag) phase as it begins 10-11 days post-anthesis (MacGregor et al., 1971, Gallagher et al., 1976). This phase is characterised by cell growth and differentiation (Kirby et al., 1984). During this phase, sucrose is being converted into starch (Baxter and Duffus, 1973, Cerning and Guilbot, 1973, Brooks et al., 1982). Starch comprises 60-75% of mature grain weight (Duffus and Cochrane, 1992), with studies showing that starch synthesis and total dry matter accumulation are limited by reactions involved in starch synthesis rather than the supply of assimilates during this phase (Lingle and Chevalier, 1984, MacLeod and Duffus, 1988). The growth rate during this period can be linear (Smith et al., 1999) and is capable of exceeding the total growth rate of the crop. Therefore it has been suggested that there is remobilisation of reserves stored pre-anthesis to the growing grain (Gallagher et al., 1976). The final phase of the grain filling period, grain ripening (dehydration), begins once dry matter accumulation has ceased. Dehydration occurs at the top of the ear and moves towards the base, some have suggested that this is due to change in the vascular tissue along the rachis (Cochrane, 1985). Once the grain has dehydrated to the desired moisture content, it is

then harvested, in cool temperate climates the grain filling phase can last from 24-51 days (Gallagher et al., 1976, Bingham et al., 2007b, Newton et al., 2011).

The rate at which the plant goes through this life cycle is mainly determined by temperature unless it is exposed to stresses such as extreme levels of disease or weather events (Hay and Porter, 2006). The base temperature required for development is generally in the range of 0-5 °C and the rate of development increases linearly until it reaches the optimum range (20-30 °C) (Jame et al., 1999). Within this linear phase, the plant cannot distinguish between 5 °C for 20 hours from 10 °C for 10 hours (Hay and Porter, 2006), although extreme events such as temperatures below the base temperature or disease will cause the phase to move away from linearity (Jame et al., 1999). Vernalisation and photoperiod influence the rate of development (Miralles and Richards, 2000). Photoperiod acts as an environmental cue to signal reproductive development of the plant (Hay, 1990). Vernalisation is defined as the induction of flowering by exposure to an extended period of low temperature (von Zitzewitz et al., 2005). The requirement for vernalisation supersedes the long day (photoperiod) flowering response (Hemming et al., 2008), and also will not allow the plant to move from the vegetative phase to the reproductive phase without the exposure to a cold period (Sasani et al., 2009). These two factors are vital for winter varieties as they ensure that flowering is delayed until after winter, reducing the risk of frost damage (Limin and Fowler, 2006).

1.2 Barley Classification

Barley can be classified into different groups based on features such as spike type (two and six-row), growth habit (winter or spring) and breeding method (hybrid or conventional). Winter or spring varieties are categorised based on their response to the environment. Winter varieties require a vernalisation period in order to enter the reproductive phase (Limin and Fowler, 2006), whereas spring varieties do not require this exposure to a cold period in order to reach anthesis (von Zitzewitz et al., 2005).

Wild barley is a two-rowed type of barley and is the progenitor of cultivated barley (von Bothmer et al., 1995, Zohary et al., 2012). The development of the six-row spike is controlled by a single allele *vrs1*, which is recessive to the dominant allele responsible for the two-rowed spike *Vrs1* (Lundqvist et al., 1997). It is assumed in the literature that six-row barley developed from domesticated tow-row barley through a spontaneous mutation (Dickson, 1979, Komatsuda et al., 2007, Zohary et al., 2012).

The differentiation of the row type occurs during the spikelet development phase. Bonnett et al. (1966), found that there was no difference in the apical development of two and six-row types up until the point where the stamens began to differentiate. This point is where differences start to be seen, the difference begins with the development of the lateral spikelets at each rachis node. In two-row types the lateral spikelets develop very slowly, fail to produce an awn and are infertile (Bonnett et al., 1966, Kirby et al., 1984, Komatsuda et al., 2007), while the lateral spikelets on the six-row type develop to produce grain, albeit at a slower rate compared with the central spikelet (Bonnett et al., 1966, Komatsuda et al., 2007).

Hybrid breeding has been a topic of many investigations in cereal crops, due to the success of hybrid breeding programmes in crops such as maize, sunflower and sugar beet (Pandey, 2002). There has been some evidence of increased utilisation of farm-saved seed, hybrid varieties prevent this as there is an inbreeding depression, thus increasing the return on investment to seed companies (Edwards, 2001). However, there have been issues with hybrid breeding in cereal crops, such as lower heterosis compared to other crop types and also difficulties implementing seed production (Oettler et al., 2005, Edwards, 2001, Lu and Xu, 2010). The most widely used mechanisms which facilitate hybrid breeding in cereal crops are; 1) chemical hybridisation agents, which are chemicals that cause male sterility when applied to crops. 2) Cytoplasmic male sterility (CMS), which is a genetic trait that causes the male sterility, allowing for the female parts to be fertilised by pollen from another line (Longin et al., 2012).

Traditionally, conventional line varieties have dominated, but in recent times there has been renewed interest in F1 hybrid seed production. Hybrid breeding in barley began when the first male sterility gene was discovered in 1940 (Suneson, 1940). Hybrid varieties soon became popular in Arizona with 12-20000ha grown annually due to their 15-20% yield advantage over conventional line varieties (Ramage, 1983), although this utilisation ceased with the introduction of semi-dwarf varieties in the 1970s which closed the yield gap between hybrid and conventional varieties. In 1979, Ahokas (1979) discovered a CMS system with a reliable single dominant restorer gene in barley and in 1994 Paul Bury, a breeder at Syngenta seeds started to utilise this CMS system to produce hybrid six-row barley varieties (Longin et al., 2012). The first commercial variety was released in 2002, with more than ten varieties released onto the market currently (Longin et al., 2012). Initial

results of these hybrid barleys have shown that they produce higher yields and improved yield stability compared to conventional two and six-row varieties (Mühleisen et al., 2014). This higher yield potential is reflected in the national recommended list trials conducted in the UK by the AHDB and the department of agriculture in Ireland (AHDB, 2018, Anon., 2017). A seed production company (Syngenta, Basel, Switzerland) has a scheme in the UK where if the hybrid barley does not achieve higher yield compared to the conventional variety they will provide financial reimbursement to the grower (Hill, 2015).

1.3 Source and sink

The source-sink relationship determines plant growth throughout the whole life cycle of the plant (Yu et al., 2015). Source organs export assimilates to importers of assimilate, called sinks (Braun et al., 2014). During germination energy stored in the endosperm (source) is utilised by the developing embryo (sink) for growth, when the plant transitions into the vegetative phase the plant relies on energy produced by mature leaves to supply developing leaves and tillers with assimilate. During the reproductive phase, nutrients are exported from source organs to the developing ear (Yu et al., 2015). In source leaves, assimilates are produced by the process of photosynthesis. The production of assimilate is carried out in the mesophyll cells of the leaf where solar energy is used to fix carbon, forming large carbon compounds (Lincoln and Eduardo, 2006) mainly sugars, with sucrose being the primary sugar produced (Yu et al., 2015).

The phloem provides the link between the source and sink organs within the plant (Lemoine et al., 2013). The phloem transports assimilate by an osmotically generated pressure difference between source to sink organs (Lemoine et al., 2013, Ruan, 2014, Yu et al., 2015). There are a series of sink organs within a plant competing for a fixed amount of assimilates produced by the source organs, thus creating a priority system among competing sinks (Lemoine et al., 2013). The ability of these sink organs to compete for assimilates known as sink strength (Bihmidine et al., 2013). How this assimilate is partitioned is critical in determining crop yield (Patrick, 1997, Ruan et al., 2005). This allocation can be described in harvested crops as harvest index (HI), a high HI would indicate that a large amount of assimilates was partitioned to the harvested parts of the plant indicating a high sink strength of these sections (Gifford et al., 1984). Yield increase over the last 50 years has in part been attributed to the improved partitioning of assimilate into harvested parts (grains) (Reynolds

et al., 2005, Newton et al., 2011). It is accepted that there is limited scope for further increases in HI due to the need to maintain leaf area and stem biomass for interception of solar radiation (Cassman, 1999).

For the purpose of this project from now on source will be the defined as the production and remobilisation of assimilates for grain filling, while sink capacity will be defined as the number of grains per unit area and by the storage capacity of those grains.

1.3.1 Sink capacity

As yield in most cereals has been found to be sink-limited (Borrás et al., 2004, Bingham et al., 2007a, Miralles and Slafer, 2007, Serrago et al., 2013), thus the formation of sink capacity is vital in the determination of yield. Sink capacity is made up of two components 1) the number of grains per unit area and 2) the storage capacity of these grains.

The number of grains per unit area itself is made up of two subcomponents, namely the number of ear bearing shoots per unit area (ears m^{-2}) and the number of grains per ear (grains ear^{-1}), while the number of grains ear^{-1} consists of the number of fertile spikelets ear^{-1} that are fertilised at anthesis and become mature grains at harvest. Early in development, when the young ear is still at ground level (pre-stem extension) the initiation of both these components has taken place, thus at this early stage, the maximum number of grains per unit is determined although the development and survival of these components are crucial in the determination of the yield at harvest.

The number of ears m^{-2} is a critical component to barley yield in high yielding environments (Kennedy et al., 2016). The number of ears m^{-2} is made up of the number of fertile tillers and main stems m^{-2} that produces ears that reach maturity. Tillering is divided into two phases, an initiation and emergence phase followed by a period of tiller death (Garcia del Moral et al., 1984). The emergence of the first tiller occurs when the third leaf has emerged from the plant (Kirby et al., 1984, Slafer et al., 2009). Tillers emerge in a consistent pattern, which is closely related to the emergence of leaves on the main plant (Kirby et al., 1985). The typical tillering pattern is a rapid increase in number during the vegetative phase, with maximum tiller number generally being reached around the start of stem extension followed by a period of tiller mortality (Kirby et al., 1985, Garcia del Moral et al., 1984). However,

recent evidence shows that this pattern can be quite variable across sites and years (Kennedy et al., 2016). For example tillering can resume after anthesis if conditions are suitable (Kirby, 1967, Aspinall, 1961), although it has been shown these late tillers make no significant contribution to yield (Kennedy et al., 2016). Two- and six-rowed varieties differ in their tillering capacity with two-row varieties generally having a higher tillering capacity compared with the six-row types (Kirby and Riggs, 1978, del Moral and del Moral, 1995, Garcia del Moral et al., 2003). Management practices such as nitrogen fertilisation (Garcia del Moral et al., 1984, Wamser and Mundstock, 2007), growth regulation chemicals (Smith et al., 1999) and the control of early-season disease (Lim and Gaunt, 1986) have been shown to increase tiller survival.

As mentioned above the production of spikelets follows a similar pattern to that of tiller production, a period of initiation followed by a period of death. Once the formation of the ear is complete some of the initiated spikelets will die off during stem elongation and prior to anthesis (Gallagher et al., 1975, Kirby et al., 1984, Waddington et al., 1983). Six-row varieties produce more fertile spikelets/floral primordia per ear (Kernich et al., 1997, Miralles et al., 2000, Arisnabarreta and Miralles, 2006), but mortality is higher in six-row compared to two-row varieties (Arisnabarreta and Miralles, 2006). Mortality rates of 42% and 56% have been reported for six-row varieties compared to rates of 30% and 37% presented for two-row varieties (Arisnabarreta and Miralles, 2006, Alqudah and Schnurbusch, 2014). Reasons suggested for this increased mortality is the larger sink capacity in six-row varieties, thus creating greater competition within the ear for resources leading to a higher abortion rate (Appleyard et al., 1982). Arisnabarreta and Miralles (2006) and Miralles et al. (2000) explained differences in spikelet mortality based on spikelet structure and position, both of these authors noted that six-row varieties have smaller carpels, suggesting this as a reason for the increased mortality. They also found evidence of reduced synchrony between the tip, basal and central sections of the two-row apex, therefore spreading the demand for assimilates over a longer period, increasing survival. Alqudah and Schnurbusch (2014), presented an alternative theory, proposing that the reason for improved survival in two-row varieties may be due to separated vascular bundles between the rachis and distal spikelets similar to wheat.

The period of spikelet mortality can run parallel to the period of tiller death. This period coincides with the stem extension period, where the canopy is expanding rapidly, thus

significant spikelet mortality can occur due to a limitation in assimilate supply (Arisnabarreta and Miralles, 2008a). Avenues for reducing spikelet mortality have been suggested such as; the lengthening of the stem extension period (Miralles et al., 2000, Miralles and Slafer, 2007, Reynolds et al., 2009), reducing the speed of floret development (Miralles and Slafer, 2007), and increasing pre-anthesis RUE to increase the assimilate availability (Reynolds et al., 2009).

Arisnabarreta and Miralles (2008a), used shading treatments on isogenic lines of two and six-row barley to establish the critical period for grain number establishment. In this study, four shading treatments were used at various stages during development with the authors concluding that the crucial period for grain number determination appears to be the period close to heading but maybe slightly earlier in two-row (40-10 days prior to heading) than the six-row barley (30 days until heading). Therefore, it is clear that the period from the onset of stem extension to anthesis is critical in the formation of the number of grains per unit area in barley

When discussing sink capacity, a component which is often overlooked is grain storage capacity or in this case potential grain weight (PGW). PGW can be affected by both pre and post-anthesis conditions. Bingham et al. (2007b), found that there was a positive relationship between the amount of light intercepted after anthesis and mean grain weight (MWG) indicating that this phase may be important in determining final grain size. Endosperm cells which contribute to the storage of starch have been shown to cease forming 14-23 days after anthesis (Cochrane and Duffus, 1983, Kvaale and Olsen, 1986). The number of cells formed in this period has been shown to have a positive correlation on the final grain weight in barley (Cochrane and Duffus, 1983). There is increasing interest in the role of the seed coat or pericarp in the control of seed size as it has been reported that water and nutrient supply occurs via the seed coat (Radchuk and Borisjuk, 2014). At maturity, the endosperm makes up the majority of the final grain weight, during the period of endosperm cell number formation the pericarp is the major tissue of the grain (Radchuk et al., 2017). Several genes which have been associated with seed size in *Arabidopsis thaliana* are expressed in the seed coat (pericarp) (Roszak and Köhler, 2011). Genes that are suspected of controlling endosperm cell number are strongly transcribed in the pericarp while weakly transcribed in the endosperm (Izawa et al., 2009). In a recent study, Radchuk et al. (2017), confirmed that programmed cell death in the pericarp determines endosperm size (number of cells) and final

grain weight, through timely death of cells to allow for assimilate supply and space for the expanding endosperm.

The relationship between carpel weight at anthesis and potential grain weight has received attention in the literature. Xie et al. (2015), measured carpel weight, grain dry matter and water accumulations, grain dimensions, flag leaf senescence and de-graining at anthesis in wheat in the field. The authors presented findings of a strong positive association between carpel dry weight and final grain weight. Larger carpels contributed to higher initial grain filling rates, while carpel size had little effect on the rapid grain filling rate, interestingly larger carpels were negatively correlated with late grain filling rate. Hasan et al. (2011), finding's agree with the above, carpel weight was strongly and positively associated with final grain weight in two wheat varieties with differing grain weight potentials. In the same study, carpel weight at anthesis was positively associated with grain volume, water content and length. Final grain weight was also positively related to ovary weight in sunflower (Castillo et al., 2017). Benincasa et al. (2017), investigated the relationship between carpel size and grain size under different plant densities and seeding rates. The results showed that carpel size responds to such conditions to a larger extent (10 fold) than grain size (0.5 fold). The authors suggested that once carpel size is matched to source availability the plant adjusts mostly grain number resulting in a more conservative grain size, although the question remains whether grain size is sink- (genetic control) or source-limited. Guo et al. (2016), related carpel size (width measured) of florets in distal positions to the number of grains per ear, suggesting that assimilate allocated to distal florets may play a critical role in regulating grain set in wheat. While position within the floret is an important factor, findings in wheat suggest that carpels in florets further from the rachis were found to be lighter than those closer to the rachis (Xie et al., 2015, Hasan et al., 2011, Guo et al., 2016). Although Arisnabarreta and Miralles (2006), suggested carpel weight as a reason for the increased spikelet mortality in a six-row compared to a two-row variety no evidence was provided on whether the authors actually measured the weight of the carpels, whilst no other authors have investigated if carpels in the lateral positions in the six-row spike are lighter compared to the carpels in the central positions.

1.3.2 Source

The main supply of assimilate during the grain filling period comes from the conversion of CO_2 into fixed carbon through the use of light energy in photosynthesis, stored reserves can also be remobilised and used to supply developing sinks with assimilate (Juchaux-Cachau et al., 2007). The factors which influence the quantity of source available during grain filling are the ability of the crop canopy to intercept light, the efficiency with which this energy is used to produce biomass and the amount of stored reserves remobilised during grain filling.

The proportion of incident radiation that is intercepted by the crop canopy is a function of its size and architecture (Bingham and Newton, 2009). Leaf area index (LAI) is defined as the ratio of leaf area to ground cover and is a popular measure of the size of crop canopies (Cowling and Field, 2003). Large canopies will intercept a larger fraction of the light than smaller ones, with cereal canopies having the ability to intercept up to 95% of incident radiation (Sylvester-Bradley et al., 1990). Different crop species, for example, oilseed rape which has a different branching pattern, leaf shape and size, can intercept larger fractions of the incident radiation with smaller canopies (Berry and Spink, 2006). Architectural traits such as leaf shape, leaf size distribution, leaf angle of inflection, and surface characteristics influence how much light is transmitted and reflected within the canopy (Kramer et al., 1980). Canopies with more erect leaves allow more light to be intercepted lower in the canopy (Bingham and Newton, 2009). The duration of the canopy is fundamental to the total amount of light that the crop can capture during the grain-filling period. Methods such as the use of fungicides to protect the canopy from late-season disease or delaying canopy senescence (Wu and von Tiedemann, 2001, Weisz et al., 2011) using 'stay-green' traits have been used as avenues to extend canopy duration (Gous et al., 2013).

Radiation use efficiency (RUE) is the efficiency with which a crop converts light energy into biomass. Bingham et al. (2007a), presented values for RUE in winter barley ranging from 2.0 - 3.8 g MJ^{-1} of PAR which is some way off the theoretical limit proposed by Loomis and Williams (1963), thus there is scope for RUE to be increased. The greatest potential for increasing RUE reported in the literature is the alteration of the source-sink balance (Newton et al., 2011). Yield in barley is sink-limited (Bingham et al., 2007a, Serrago et al., 2013). Wheat yield has also been shown to be sink-limited (Reynolds et al., 2005, Borrás et al., 2004), but to a lesser extent compared to barley (Serrago et al., 2013). Bingham et al.

(2007a), suggested the presence of feedback inhibition of RUE during the later stages of grain filling, reducing RUE below its potential. Thus, it may be possible to increase RUE during grain filling through increasing the number of grains set and the storage capacity of these grains, negating the feedback inhibition of photosynthesis, this would increase HI and the overall yield potential of the crop (Newton et al., 2011).

Cereals have the ability to utilise stored reserves in the form of water-soluble carbohydrates (mainly fructans) deposited in the stem and leaf sheaths prior to grain filling which can then be translocated to the grains (Gallagher et al., 1975, Foulkes et al., 2007). Translocation of these reserves can act as a buffer for grain yield in conditions which are not favourable for photosynthesis (Gallagher et al., 1976). Contribution of these reserves to final yield in wheat has been shown to be 20% in non-stressed conditions and up to 70% in stressed conditions (Goggin and Setter, 2004, Blum, 1998). For barley, it has been shown that 1-3 t ha^{-1} of dry matter can be stored in the stems, which can contribute anywhere from 11-45% of final grain yield (Bingham et al., 2007a).

1.3.3 Investigating the source-sink balance

The most common method reported in the literature to investigate the source-sink balance in cereal crops has been manipulation of the source-sink ratio during grain filling. A compressive review was conducted by Borrás et al. (2004), of the effect of assimilate manipulations during grain filling on seed dry weight in wheat, soybean, and maize across a wide range of environments. The review concluded that grain filling in wheat was, in most cases more sink-limited than source-limited, while soybean had a large degree of co-limitation. A co-limitation is when the change in grain weight does not match the relative change in assimilate supply (Borrás et al., 2004). The findings on maize showed that grain weight was dramatically reduced if the availability of assimilates was decreased while there was a lack of response when assimilates were increased.

Shading of the crop canopy has been a popular method to investigate the source-sink balance. Shades are placed above the crop, reducing the amount of photosynthetically active radiation (PAR) that the crop can intercept, thus reducing the amount of energy available for assimilate production. However, shading the crop canopy can cause unintentional effects, such as the creation of a microclimate. For example, the relative humidity and temperature under artificial shades have been found to be higher compared with field-grown crops of ginseng

(Asseng et al., 2017). In spring barley shading of the crop, canopy was found to raise the temperature by 0.4 °C and resulted in a 0.3% rise in relative humidity (Kennedy, 2015). The same study also noted that soil moisture was affected by shading, increasing in one season and not changing in the following season.

Shading has been used in barley (Serrago et al., 2013), wheat (Caldiz and Sarandón, 1988, Fischer and HilleRisLambers, 1978, Serrago et al., 2013) and soybean (Andrade and Ferreiro, 1996, Egli and Bruening, 2001). Serrago et al. (2013), conducted two types of shading on barley and wheat, one was the traditional shading of the entire canopy using a 75% light reducing shade, while the other just shaded the leaves with the spike remaining above the shade. Both treatments were imposed seven days post-anthesis and remained for the duration of grain filling. Whole canopy shading reduced final grain weight by on average 35% across wheat and barley at two sites, in a low and a high input programme. Partial shading of the canopy only reduced grain weight by 20% across the same treatments. The reason for this was that spike photosynthesis was up-regulated to supply additional assimilates. The authors concluded that source limitation of these crops would be a crop condition which only rarely takes place due to the remaining reserves left in the stems at maturity and the ability of the spike to up-regulate its photosynthetic capacity (Serrago et al., 2013). However, it must be noted that these experiments were carried out in Spain where light availability during the grain filling period is high.

De-graining has also been a popular method for manipulating the source: sink ratio. This is a method of increasing assimilate supply per grain by reducing the size of the sink. Authors have investigated effects of de-graining on wheat (Calderini and Reynolds, 2000, Acreche et al., 2009, Cartelle et al., 2006) and barley (Voltas et al., 1997, Dordas, 2012, Serrago et al., 2013). Calderini and Reynolds (2000), conducted de-graining in wheat varieties at heading and seven days post-anthesis, finding a significant increase in grain weight in plants de-grained at the heading stage while there was no response to treatments imposed post-anthesis in one experiment and a decrease in grain weight after post-anthesis de-graining in an. Acreche et al. (2009), compared the source-sink relationship in modern and older varieties, trimming of the upper half of the spike 7-10 days post-anthesis. The findings showed that the modern varieties displayed a co-limitation, while the older varieties were more sink-limited. Serrago et al. (2013), investigated the effects of de-graining wheat and two-row barley finding a significant increase in final grain weight after spikelet trimming in

wheat, while there was no effect on grain weight in barley. Voltas et al. (1997), also used de-graining to assess the source-sink balance in modified main stems only across three six-row barley varieties finding an average of a 20% increase in final grain weight from the treatment suggesting that grain filling was source-limited in this experiment. It must be noted that these authors used different methods of de-graining. Voltas et al. (1997), pierced the carpels of the lateral spikelets on one side of the spike and the corresponding central spikelet on the opposing side of the spike at the time of anthesis, whereas Serrago et al. (2013), simply trimmed the top half of the spike off 7 days after flowering had occurred. The time of imposition of treatment may have affected the results presented by Voltas et al. (1997), by modifying the source-sink ratio during the lag phase of grain filling, when endosperm cells per grain and thereby potential grain weight is determined (Schnyder and Baum, 1992, Nicolas et al., 1985). Conversely, Serrago et al. (2013), avoided this period by imposed treatment 7 days after anthesis. The above explanation may also give reason to the finding presented by Calderini and Reynolds (2000), where de-graining conducted at anthesis significantly reduced grain weight at harvest whereas de-graining conducted seven days post-anthesis had no significant effect on final grain weight.

Methods of increasing assimilate supply per grain in a non-destructive way are rare in the literature. Kennedy (2015), used a means of increasing light interception to a single row. The method involved pushing back adjacent rows along a 4 metre length using a system of rope and small wooden fencing stakes. This allowed more light to be intercepted by a single row as the competition for light from the adjacent rows is reduced. In the above study, this method was used to investigate the effect on potential grain weight of assimilate supply immediately post-anthesis for a two week period, with the adjacent rows closed in after the two week period. Similar methods of increasing incident radiation received by the crop have been published, such as placing light reflectors between the rows of maize, showing an increase in yield (Schoper et al., 1982).

Defoliation is another popular post-anthesis manipulation method to investigate source-sink relationships. This method involves removing leaves in order to reduce the plant's capacity to produce assimilates, affecting the availability of source, thus reducing the source: sink ratio. Dreccer et al. (1997), investigated the effect of defoliation in spring barley using a pot study, the defoliation method used involved removing alternating leaves beginning at the leaf below the flag leaf and working down the canopy. The treatments were imposed five

days post-anthesis. The results reported were that there were no effects on final grain weight. In the review carried out by (Borrás et al., 2004), two studies investigated post-anthesis defoliation in wheat. Kruk et al. (1997), studied the response of seed dry weight to post-anthesis defoliation in varieties released from 1920 to 1990 in field conditions, the results showed that grain weight was unaffected by defoliation in the old varieties, whilst defoliation caused a significant reduction in grain weight in the modern varieties at several positions on the spike. Simmons et al. (1982), used defoliation to test seed dry weight response in spring wheat varieties. Defoliation treatments were imposed at anthesis and 14 days post-anthesis, the findings showed that defoliation caused a significant reduction in seed dry weight compared to controls in both treatments times, although the treatment at anthesis had larger effects.

Most of the authors who have investigated source-sink manipulations have done so on healthy plants. As discussed earlier grain filling can be divided into three distinct phases, the lag phase where endosperm cell division is taking place, the active grain growth phase in which sugars are being synthesised into starch and a period of rapid dehydration/ripening. Manipulations of source-sink ratios during the first two phases could have opposing effects on the response of the remaining grains. If de-graining was imposed at anthesis, then this could theoretically increase the availability of assimilates to remaining spikelets during early grain development when grain weight potential is being determined therefore increasing individual grain weight via an increase in their storage capacity. Conversely, if de-graining is imposed after the lag phase, then this reduces the number of grains but after the grains have set their individual storage capacity. If late-season disease occurs in the crop, then this could have effects on both phases of grain filling. Serrago and Miralles (2014), investigated the effect of source-sink manipulations in a diseased and healthy crop. The study was conducted on wheat and found that a de-graining treatment increased grain weight in an infected crop, but grain weight was unaffected in a healthy crop. The authors concluded that disease does, in fact, affect the source-sink balance, changing grain filling from a state of sink limitation in a healthy crop to one of source limitation in a crop with disease.

The above methods can be difficult to interpret, as a large change in assimilate supply may lead to significant but small changes in MGW. This would imply a source or co-limitation, but a quantitative assessment of the degree of limitation is difficult. An alternative method to investigate the source-sink balance is to estimate the potential assimilate supply per grain

during grain filling, via measurements of the light interception by the crop, calculating the radiation use efficiency and measuring the amount of water-soluble carbohydrates at anthesis and comparing this estimation to the achieved grain weight as described by Bingham et al. (2007a). This method allows for a more quantitative interpretation of the source-sink balance during grain filling.

1.4 Disease management

Disease management is a crucial part of crop husbandry in Western Europe as climatic conditions in this region create ideal conditions for the spread of fungal pathogens with studies showing that atmospheric moisture is the single most important environmental factor governing the severity and incidence of fungal disease on plants (Burdon, 1991). High relative humidity and several hours of free surface water are critical for both spore germination and successful infection (L Huber and Gillespie, 1992). Studies investigating the growth of fungi on plants in a field environment have shown that fungal growth is favoured by high moistures and moderate temperatures (Colhoun, 1973, Griffin, 1996). Although these are general conditions conducive to fungal pathogen spread, specific diseases will differ in the climatic conditions suitable for their spread, these conditions for the diseases which affect barley are discussed below. Temperate climates favour growth of most fungi but the most common foliar diseases that affect barley are Rhynchosporium leaf scald (*Rhynchosporium commune*) and powdery mildew (*Blumeria graminis* f. sp. *Hordei)* (Bingham and Newton, 2009), whilst ramularia leaf spot (*Ramularia collo-cygni*) has become a significant disease in recent times (Havis et al., 2015).

It is estimated that pathogens reduce the global harvest by between 10-16% annually (Oerke, 2006). This threat is amplified when the development of pesticide resistance is considered, plant pathogens can develop resistance to single or numerous fungicide groups rapidly due to selective pressure during reproduction (Dooley et al., 2016). In wheat it has been reported that septoria tritici blotch (*Zymoseptoria tritici*) has shown decreased sensitivity to the azole (Cools and Fraaije, 2013), Quinone outside inhibitor (Fraaije et al., 2005) and succinate dehydrogenase inhibitor (Dooley et al., 2016) fungicide groups significantly threatening wheat production globally.

The impact of fungal pathogens could also increase due to the effects of climate change. Increased CO_2 levels caused by climate change may affect the performance, prevalence and

distribution of plant pathogens (Chakraborty et al., 2008). Elevated CO_2 levels can increase the growth of some fungal pathogens (Coakley et al., 1999, Chakraborty et al., 2000), while an increase in plant biomass (caused by increasing CO_2 levels) accompanied by an increase in humidity within the canopy can increase the infection and size of plant pathogens (Manning and Tiedemann, 1995, Mitchell et al., 2003, Pangga et al., 2004). Changes in rainfall patterns and temperature increases could conceivably alter land use leading to new plant pathogen problems (Parker and Gilbert, 2004). Climate change could also alter the growing season of crops, milder winters could lead to the growing seasons of winter crops beginning earlier, increasing the yield loss risk from early disease infection.

Policy influences could increase the threat of fungal pathogens to food security, especially in the EU. Directive 2009/128/EC on the sustainable use of pesticides and Regulation (EC) 1185/2009 aimed at obtaining pesticide usage data have both been introduced to decrease the use of conventional pesticide in European agriculture (Hillocks, 2012). It was estimated that Regulation 1185/2009 could lead to the loss of up 30% of the active ingredients on the market (Jess et al., 2014). The reason for this has been attributed to a shift in the risk evaluation of pesticides during the registration process in which, in addition to the risk assessment to human and environmental health, the potential 'hazard' to human or environmental health is also considered (Jess et al., 2014). A report carried out on the potential impact of the loss of the azole group, which are under threat under the new directives, on wheat production in Europe concluded that the result of a withdrawal of the azole group would lead to a loss of 4.6 billion euros in 2020 while it would also mean that the EU would no longer be self-sustainable in wheat production (Di Tullion et al., 2012). However, Di Tullion et al., (2012), carried out this study in 2011, since then resistance to septoria has developed, which may impact the conclusion. Another report on the potential impact of the loss of chlorothalonil (multisite fungicide) (which has now been removed from the market) concluded that net margin for Irish farmers would be reduced by 50% and 65% for wheat and barley respectively, while also stating that cereal production will only be economical in the highest yield potential sites with a low cost of production (Kildea et al., 2018).

The above-mentioned EU directive also brought into law that the control of pests must be carried out within an integrated pest management (IPM) strategy. Pesticides must be used in a sustainable way, a method of doing such is only using pesticides when necessary, and when

other solutions are not available. The necessary use of pesticides can be expressed in terms of likely improvement in yield or quality (Bingham et al., 2014). In wheat grain quality can be diminished by aphid feeding during grain filling (Wratten, 1975), these aphids can be controlled by an insecticide, although the application may only take place if the number of aphids on the wheat spike exceeds a threshold, which is determined by scientific studies (Larsson, 2005). The sustainable use of fungicides can be achieved by utilising scientific evidence on the periods in a crop's lifecycle, which are critical to yield formation to target application timing.

1.4.1 Important diseases in barley

Rhynchosporium commune is the pathogen that causes Rhynchosporium leaf scald (Rhynco) in barley. This pathogen can cause dramatic yield reductions, up to 40%, along with reductions in grain quality (Shipton et al., 1974). Sources of primary infection include crop debris (Zhan et al., 2008), seed-borne infection (Atkins et al., 2010, Zaffarano et al., 2006) and windborne ascospores (Fountaine et al., 2010). Secondary infection mainly occurs via splash dispersed conidia (Fitt et al., 1989). Interestingly it has been recently reported that the pathogen can infect seeds without the appearance of visual symptoms (Atkins et al., 2010, Fountaine et al., 2010).

Net blotch disease of barley is caused by the fungal pathogen *Pyrenophora teres.* There are two forms of the fungus, the spot form (*P. teres f. maculate*) and the net form (*P. Teres f. teres*). Yield reductions caused by the infection of this pathogen have been reported to be as high as 44% for the spot form (Jayasena et al., 2007) and 56% for the net form (El Yousfi and Ezzahiri, 2002). While, the initial symptoms of both forms are similar, the spot form produces circular or elliptical, brown necrotic lesions while the net form forms distinctive dark-brown necrotic lesions with netted patterns (Lightfoot and Able, 2010). The life cycle of both forms is almost identical except that the spot form is not known to be carried over in infected seed (Liu et al., 2011, Leisova et al., 2006). The primary source of inoculum is ascospores and conidia which survive as pseudothecia on the surface of infected stubble.

Ramularia leaf spot (RLS) caused by the fungus *Ramularia collo-cygni* has become an important pathogen in barley in recent times, with a lot of focus on all aspects of the host, pathogen and environment being studied (Havis et al., 2015). The relatively recent focus on

RLS has been attributed to confusion with other pathogens and physiological spotting on leaves (Havis et al., 2015). Yield losses have been reported as high as 70% during seasons of high pressure in susceptible varieties (Clemente et al., 2014, Pereyra, 2013). The climatic conditions which favour the spread and development of RLS are conditions of high relative humidity leading to prolonged periods of leaf surface wetness (Havis et al., 2012), while radiation intensity has been shown to be less critical (Formayer et al., 2004). There has been much debate about the primary source of inoculum, in recent times there has been confirmation of transmission from infected seed (Havis et al., 2014b, Matusinsky et al., 2011). Symptoms of RLS generally appear post-flowering and are described as small brown-blackish spots which form a chlorotic halo with lesions combining to create a larger necrotic lesion (Havis et al., 2014). Similar to Rhynco the fungus can grow within the plant during the pre-anthesis period without showing visual symptoms (Havis et al., 2014).

Powdery mildew's (*Blumeria graminis* f. sp. *Hordei)* are known as some of the most common plant pathogenic fungi (Glawe, 2008). *Blumeria graminis f. sp. Hordei* is the fungus, which caused powdery mildew in barley (Dean et al., 2012). Yield losses of up to 40% have been reported due to infection of powdery mildew in barley (Chaure et al., 2000). The disease is more prevalent in regions of temperate climates, which have higher humidity (>95%) and cooler temperatures (10-22 °C) (Wiese, 1987, Jones and Clifford, 1983). The primary source of inoculum is wind-dispersed conidia (Zhang et al., 2005).

Fusarium head blight (FHB) is a disease more associated with wheat and other cereals but can also infect barley (McMullen et al., 2012). The disease is caused by a complex of fungal pathogens which can vary with geography (Xu and Nicholson, 2009). The species of fungi which are present in Europe are *Fusarium graminearum, Fusarium culmorum, Fusarium avenaceum, Fusarium poae, Microdochium majus, and Microdochium nivale* (Xu et al., 2005). Conditions for infection require moisture and high temperature at anthesis for infection to occur (Xu, 2003). FHB can reduce yield and quality of the grain (McMullen et al., 2012) in addition, an infection can also lead to a range of mycotoxins being produced in infected grains (Bottalico and Perrone, 2002). These mycotoxins cause the grain to be unsuitable for human or animal consumption (Miller, 2008).

Stagonospora (Septoria) nordorum is a major pathogen of wheat, causing the disease Septoria nordorum blotch (SNB) as well as glume blotch (Solomon et al., 2006). Much of

the literature investigating SNB focuses on wheat, *S. nordorum* can also infect barley (Solomon et al., 2006). Newton and Caten (1991) suggested that the types of *S. nordorum* that infect wheat and barley are genetically distinct populations within the species. Yield losses have been reported as high as 31% in wheat (Bhathal et al., 2003), although reports of yield losses in barley in the literature were not found. Visual symptoms on leaves are overall-shaped light brown lesions, pycnida are produce following about 7 days of humid conditions after lesion appearance (Solomon et al., 2006). Pynindia are translucent are first then expand to form pale brown growths (Douaiher et al., 2004). The primary source of inoculum is both infected seed and air borne-ascospores (Shah et al., 1995, Shah and Bergstrom, 2000). Low temperature and high rainfall has been shown to trigger the release of ascospores from the previous crops debris (Bathgate and Loughman, 2001). *S. nordorum* enters the plant by directly penetrating the cuticle (Karjalainen and Lounatmaa, 1986), then colonising the host cell leading to the cell collapsing and the formation of pyninda through asexual reproduction (Eyal, 1987). Asexual reproduction is said to be characterised by patterns of rainfall every 2-3 days every 8-12 days (Bathgate and Loughman, 2001). The secondary source of infection is rain splash spread of spores within the canopy (Shah et al., 2001).

1.4.2 Pathogen effects on plant growth

Plant pathogens can be divided into two groups, this first being biotrophic fungi, which feed on living host tissue (Agrios, 1997), biotrophic diseases include powdery mildew (*Blumeria graminis* f. sp. *Hordei)*. The second being necrotrophs which kill host tissue and feed on the remains (Agrios, 1997), necrotrophic diseases include net blotch. Some pathogens behave as both necrotrophs and biotrophs, depending on which stage they are in their life cycle, such pathogens are called hemi-biotrophs (Glazebrook, 2005), and examples in barley are ramularia and rhynchosporium. Necrotrophs and hemi-biotrophs, reduce plant growth mainly through their effects on radiation interception, producing lesions which reduce the healthy area on the leaf surface available to intercept PAR (Bingham and Newton, 2009).

Fungal pathogens can impact plant growth throughout the entire developmental period. However, the impacts on plant growth will vary according to the developmental stage and duration of infection (Bingham and Newton, 2009). Early season infection can impact root

growth (Balasubramaniam, 1985), leaf production (Gaunt, 1995) and tiller production and survival in barley (Lim and Gaunt, 1986). As mentioned the number of grains m^{-2} is the key determinant in barley yield (Bingham et al., 2007a, Kennedy et al., 2016), the period when the number of grains m^{-2} is determined has been established as the period close to heading (Arisnabarreta and Miralles, 2008a). Therefore, infection of fungal pathogens during early stages of development will impact both the number of ears m^{-2} and grains ear^{-1} through impacts on both, tiller and spikelet production and survival. Disease infection has also been shown to impact negatively on the level of stored reserves in the stem pre-anthesis, thus reducing the amount of assimilate available for grain filling (Gaunt and Wright, 1992). These pre-anthesis effects on the plant's growth will reduce canopy size and the crops ability to intercept light, which in turn impact the development of both source, and sink prior to grain filling. As mentioned effects of pathogens are mainly through reductions in the plant's ability to intercept light, thus it not surprising that infection during the grain filling period has been shown to reduce average grain weight (Bingham et al., 2009).

1.4.3 Chemical control (fungicides)

In an IPM strategy, the use of fungicides is seen as the last line of defence (Poole and Arnaudin, 2014) and fungicides are only used to ensure protection when weakness is present in both genetic and cultural control practices (Brent and Hollomon, 2007). Although the current policy is to try to reduce reliance on conventional pesticides (Hilcokcs 2012), the use of conventional pesticides (including fungicides) is known to have many benefits including increased crop yields and improved food safety (Cooper and Dobson, 2007). Fungicides are applied to the crop in three ways; seed treatment, granular products applied to soil or foliar products applied to the crop canopy (Poole and Arnaudin, 2014). The control of foliar disease with fungicide in winter barley is carried out using foliar applications at three main timings of early spring (GS25-30), onset of stem extension (GS31/32) and awn emergence (GS49) (Walters et al., 2012, Glynn and Grace, 2017), while timings in the autumn and at full ear emergence (GS59) have had no significant effect on yield (Glynn and Grace, 2017). The GS25-29 timing provides canopy protection during tiller production. The application timing at GS31/32 is the most important application timing as the key determinate of barley yield (Bingham et al., 2012), grain number per unit area is determined following this timing (Arisnabarreta and Miralles, 2008a). The GS49 timing is the most effective timing for the

control of ramularia (Havis et al., 2015) while this timing also provides protection to the canopy during anthesis, the development of the carpel and the determination of the number of endosperm cells. The above timings reflect the finding that yield in barley is sink-limited (Bingham et al., 2007a), with a focus on pre-anthesis canopy protection. It is important to note the necessary use of fungicides, for example, fungicide applications during the winter have shown improved control of rhynchosporium compared to spring applications (Jordan et al., 1982) while timings during the winter have been shown to have no benefit to yield (Glynn and Grace, 2017).

There are four main groups of fungicides which are used for disease control in barley. (1) Quinone outside inhibitors (QoI's) (2) Sterol biosynthesis inhibitors (SBI's) (3) succinate dehydrogenase inhibitors (SDHI's) (4) multi-site inhibitors. The QoI's or strobilurin (Strob) fungicides launched in 1996 (Morton and Staub, 2008), are Group 11 on the fungicide resistance action committee (FRAC) code list. The QoI's and SDHI's (group 7) are both mitochondrial inhibitors, blocking the pathogens ability to respire (FRAC, 2018, Poole and Arnaudin, 2014). The SDHI's block specifically the ubiquinone's-binding sites in the mitochondrial complex (Sierotzki and Scalliet, 2013). The SDHI's were initially known as carboamide fungicides, with the first being released in 1966 (Von Schmeling and Kulka, 1966). These fungicides had a narrow spectrum and were mainly used as seed treatments for disease such as smuts (Sierotzki and Scalliet, 2013). The SDHI's which are used today are known as the second generation, have a much broader spectrum on plant pathogens (Glättli et al., 2011). Currently, there are 23 active ingredients listed as SDHI's on the FRAC list (FRAC, 2018). Sterol biosynthesis inhibitors include two classes of fungicides that are most commonly used on cereals, Group 3 demethylation inhibitors (DMI's) or more widely known as the azoles were first launched onto the market in 1973 (Morton and Staub, 2008) and Group 5 amines (formally morpholines (FRAC, 2018)). The azoles interact with the C14-demethylase target site, whereas the amines operate on a more limited target site within the sterol biosynthesis pathway (FRAC, 2018). Multi-site fungicides such as chloroisophtalonitriles (chlorothalonil) and phthalimides (folpet) have multiple target sites that inhibit enzymes in the fungi, eventually leading to cell death (Tillman et al., 1973). These fungicides were the first to be broadly used during the 1950s and '60s and are contact fungicides, i.e. they provide protection where the fungicide lands with no systemic activity (Gisi and Sierotzki, 2008).

1.4.4 Fungicide movement and direct effects on the plant

When applying fungicides to a crop, it is important to know how they move within and their direct effects (if any) on the plant. The first agricultural fungicides that were used were, as mentioned, contact only, and thus only had protectant activity although with the introduction of the DMI and QoI fungicides a systemic function was introduced allowing the fungicide to move into the plant, in turn providing curative activity (Chamberlain et al., 1998).

Within the fungicide groups mentioned above, there are variations with how these fungicides move within the plant. Azole's diffuse into the plant and are transported within the xylem vessels, meaning that movement is restricted to an upwards direction towards the leaf tip (Bartlett et al., 2002). This information has important practical implications for disease management, this movement of the fungicide within the plant allows the fungicide to control pathogens during their latent phase (Poole and Arnaudin, 2014), while also the direction of travel within the plant means that foliar applications cannot provide protection to leaf tissue which hasn't emerged at time of application (Bartlett et al., 2002, Poole and Arnaudin, 2014). Similar to azole, amine's and QoI's also have been found to have a systemic function with the plant (Chamberlain et al., 1998, Bartlett et al., 2002). Fungicides can also move as a vapour within the crop canopy (Poole and Arnaudin, 2014). As the SDHI's are a relatively recent addition to cereal fungicides less is known about their activity within the plant, although data from the manufacturers would suggest that they have activity both on the surface of the leaf and a systemic function depending on the host and pathogen in question (McKay et al., 2011).

In addition to controlling the fungal pathogens, some fungicides have been reported to have additional direct physiological effects. It is widely reported that the QoI fungicides can delay canopy senescence (Weisz et al., 2011), while the azole fungicide group has also been shown to have effects on delayed canopy senescence (Wu and von Tiedemann, 2001) but to a lesser extent (Bertelsen et al., 2001). Bertelsen et al. (2001), showed that QoI and azole fungicides were effective in the control of saprophytic fungi in wheat, which could explain the extension of canopy duration as these fungi have been shown to influence canopy senescence in barley (Tolstrup, 1984). Other mechanisms through which fungicides extend canopy duration have been reported, such as promoting the growth hormone cytokinin and delaying inhibitor ethylene (Grossmann and Retzlaff, 1997). The use of QoI fungicides has been reported to

improve water use efficiency under well-watered conditions, although the reverse was found in water-stressed conditions (Nason et al., 2007). Interestingly QoI's and azoles have also been found to increase the nitrogen concentration in above ground wheat tissue (Pepler et al., 2005a, Pepler et al., 2005b).

Bingham et al. (2012), presented evidence of an increase in grain numbers after application of an azole, QoI mixture in various spring barley varieties, which could not be explained either by an increase in radiation interception or the presence of visible disease. Azole's have been reported to have anti-gibberellin activity on plants (Rademacher, 2000), which in turn could have increased grain numbers through enhancement of tiller survival (Bingham et al., 2012). Mentioned above *R. commune* and ramularia both grow systemically through the plant before the appearance of visible symptoms, although the impact of this growth is not known (Walters et al., 2008), fungicides could potentially control this systematic growth (Bingham et al., 2012).

Investigating the cause of an increase in grain number after the application of azole fungicides, Bingham et al. (2014), investigated the application of a prothioconazole (azole) plus pyraclostrobin (QoI) mixture on spring barley. This study again found an increase in grain numbers in the absence of visual disease, but this increase could not be explained by the control of asymptomatic disease, the control of saprophytes or extension of canopy duration, thus concluding that the fungicides had direct physiological effects. This finding has important implications for disease control using an IPM based strategy in which monitoring for visual disease is relied upon heavily, i.e. there may be an economic return from the application of a fungicide product in the absence of visual disease. However, a recent study carried out in Ireland found no increase in grain numbers in spring barley from an application of prothioconazole plus pyraclostrobin mixture in the absence of visible disease (Doyle, 2017) with the author concluding that physiological effects may be influenced by variety, climate and soil conditions.

1.5 Knowledge gaps & Experimental objectives

Hybrid six-row varieties are relatively new to the market. Therefore very little independent research has been conducted to support current management advice, growers are reliant on

the information given by the seed suppliers. One such recommendation is a lower seed rate compared to conventional two-row varieties to take advantage of increased vigour and to offset the increased seed cost per tonne. However the agriculture and horticulture development board (AHDB) funded a study in 2006, which compared seeding rates between a conventional six-row and a hybrid six-row variety, the study found that there was no statistical difference in yield between sowing at the standard seed rate (350 seeds m^{-2}) and the manufacturers recommendation at the time (250 seeds m^{-2}) (Feer, 2006). In a recent study, results were presented which, showed under Irish conditions that breeding method or row-type had no impact on the response to nitrogen fertilisation (Hackett, 2016).

Many studies have investigated the source-sink balance in two-row barley, with the finding that yield is limited by sink capacity (Bingham et al., 2007a, Serrago et al., 2013). Questions remain as to the balance in a six-row variety with (Voltas et al., 1997) the only author to investigate the source-sink balance in a six-row. Voltas et al. (1997), concluded that yield was source limited, although it is not clear if the time of imposition of manipulation had an effect on the result. In wheat, a study conducted in the cool temperate climate of the UK suggested that the source-sink relationship operated in close balance (Beed et al., 2007), while a recent study carried out in Ireland suggested that in certain variable seasons, there is the potential for winter wheat crops to be source limited (Lynch et al., 2017a). The grains m^{-2} between wheat and six-row barley are similar, thus it is conceivable that six-row and two-row barley also differ in their source-sink balance, however, conclusive evidence to support this is currently lacking.

Response to fungicide treatment experiments has shown that pre-anthesis disease management is crucial to ensure maximum yield potential in two-row winter barley (Glynn and Grace, 2017), due to the formation of sink capacity during this period. However, it must be noted that no study has investigated the response to fungicide in a six-row variety in a high disease pressure, high yield potential environment. It is sensible to hypothesise that if a six-row variety was to be less sink-limited that a two-row variety that a different approach to disease management may be required, in which the emphasis should be placed on maximising canopy lifespan and assimilate production during grain filling rather than protection during the grain formation period.

Although the period when grain number per unit area is determined is well established (Arisnabarreta and Miralles, 2008a, Alqudah and Schnurbusch, 2014) there remain questions as to when PGW is determined. Evidence presented in section 1.5.1 shows that potential grain weight can be affected by both pre and post-anthesis conditions. Kennedy (2015), presented evidence that grain weight in spring barley was insensitive to changes in light during the two-week period post-anthesis. This would suggest that potential grain weight may be determined pre-anthesis during the same period as grains m^{-2}. It is also conceivable to consider that a six-row variety, due to greater competition within each ear may be more sensitive to changes in assimilate production during this period.

Therefore, the experimental objectives of this thesis are:

1. To test the response to fungicide timing in a conventional two-row and hybrid six-row winter barley variety under differing seed and N rates
2. To investigate the source-sink balance in a conventional two-row and hybrid six-row winter barley variety
3. To test the effect of variation in pre-anthesis assimilate supply on sink capacity formation in a conventional two-row and hybrid six-row winter barley variety.

Chapter 2 **Investigating if the optimum fungicide strategy differs between a hybrid six-row and conventional two-row winter barley variety**

2.1 Introduction

Barley (*Hordeum vulgare*) can be classified into different groups based on the fertility of the lateral spikelets, two-row varieties having sterile lateral spikelets, and six-row varieties having fertile lateral spikelets (Bonnett et al., 1966). The yield components of these two different row types differ, with studies showing that six-row varieties produce a higher number of grains m^{-2}, but with a lower average grain weight than two-row varieties (Garcia del Moral et al., 2003, Arisnabarreta and Miralles, 2015).

As mentioned in section 1.5, barley has benefited from genetic improvement in recent times with the introduction of hybrid six-row winter barley varieties. The main advantages of using hybrid varieties over conventionally bred varieties have been described as; (i) increased yield, and (ii) hybrid vigour (Longin et al., 2012, Mühleisen et al., 2013). This high yield potential has been reflected in results from both U.K. and Irish national recommended list trails where hybrid varieties have displayed higher yield potential compared to conventional two-row varieties (Anon., 2018c, AHDB, 2018).

The cool temperate climate of the UK and Ireland provides the ideal conditions for maximum yield potential of cereal crops (Kennedy et al., 2016) although these conditions are also ideal for the spread of fungal pathogens (Zhan et al., 2008). The main pathogens that infect barley in temperate climates are described in section 1.7. These pathogens can cause dramatic yield reductions of up to 70% (Shipton et al., 1974, Clemente et al., 2014, Chaure et al., 2000). The control of these potentially devastating pathogens is an essential part of agronomic management. While the use of cultural methods such as crop rotation and resistant varieties are encouraged (Clark and Hillocks, 2014) current cereal varieties still require the application of fungicide to control these potentially yield reducing pathogens (Lynch et al., 2017b).

Fungicide timing to control foliar disease infections for winter barley are focused on pre-anthesis canopy protection, with studies conducted on two-row winter barley showing the most effective fungicide timings to be at the onset of stem extension and at awn emergence

(Walters et al., 2012, Glynn and Grace, 2017). This response is unsurprising as grains m^{-2} has been shown to be the critical determinant of yield in two-row barley (Kennedy et al., 2016), with the period from the onset of stem extension until awn emergence being shown to be critical for grains m^{-2} determination (Arisnabarreta and Miralles, 2008a, Alqudah and Schnurbusch, 2014). The effectiveness of these timings is mirrored by the understanding that yield of two-row winter barley in light-limited conditions is generally limited by the number and storage capacity of the grains present (sink) at the onset of grain filling (Bingham et al., 2007a) rather than the supply of assimilate to fill the grain (source). This finding has important implications for the disease management strategy in barley as it would suggest that barley may be more tolerant of late-season disease as the supply of assimilates during the grain filling period is not crucial to the achievement of maximum yield potential, whilst infection during the period of sink formation (grains m^2 and potential grain size) has the potential to reduce yield significantly. In winter wheat (*Triticum aestivum L.*), disease management strategy is focused on protecting the upper leaves of the canopy to maximise production of assimilates during grain filling (Lynch et al., 2017c). This focus can be explained by a study conducted in the cool temperate climate of the UK which suggested that the source-sink relationship of wheat operates in close balance (Beed et al., 2007), while a recent study carried out in Ireland suggested that in certain variable seasons, there is the potential for winter wheat crops to be source limited (Lynch et al., 2017a). Therefore, protection during the grain filling period is of greater importance in a wheat crop compared to that of a sink-limited two-row barley crop.

The disease management strategy developed for two-row barley of focusing on pre-anthesis protection is currently utilised to control disease in six-row varieties, although evidence to support this strategy is currently lacking. As mentioned above, six-row varieties have different yield components compared to their two-row counterparts, producing a higher number of grains m^2 and having a lower average grain weight. These differences in yield components could lead to different disease management requi rements. It could be argued that the cause of the lower mean grain weight in six-row varieties is a shortfall in assimilate supply during grain filling due to the presence of a higher number of grains m^{-2}. If true, this would imply that six and two-row varieties have different source-sink balances, six-row varieties being less sink-limited and more limited by source than two-row varieties. This difference in source-sink balance would mean that six-row varieties are less tolerant of late-

season disease leading to a different approach to the disease management being required, in which the focus should be placed on maximising canopy lifespan and assimilate production during grain filling rather than on the development of sink capacity during the pre-anthesis period.

Increasing both seed (S) and nitrogen (N) rate has been shown to increase yield in both spring and winter barley through increases, mainly, in grains m^{-2} (Kennedy, 2015, Hackett, 2016), thus providing a mechanism in which sink capacity could potentially be increased. This increase in sink capacity may affect the source-sink balance, shifting a crop from sink-limitation under normal conditions to a source or co-limited crop due to an increase in demand for assimilate during grain filling. If true increasing S & N rate would have implications for disease management, at higher rates, the requirement for late-season disease protection could be higher due to demand for assimilate production.

In recent times, decreased sensitivity of ramularia has developed to QoI's (Matusinsky et al., 2010), azole's (Piotrowska et al., 2016) and SHDI's (Piotrowska et al., 2017), leaving chlorothalonil (CTL) as the primary method of chemical control. Ramularia effects barley during the grain filling period and has the potential to reduce yield by up to 70%, therefore effective control is vital (Clemente et al., 2014). Once the ear emergences from the leaf sheath barley are under threat of Fusarium head blight (complex of *Fusarium graminearum* and *Microdochium nivale)* (FHB) infection if conditions are suitable (McMullen et al., 2012), if FHB infection occurs, yield and hectolitre weight can be reduced (McMullen et al., 2012), while FHB can also lead to mycotoxins developing in the grain, affecting the end use (Dexter and Nowicki, 2003). Genetic resistance and cultural practices are possible control methods (Bai and Shaner, 2004), fungicides can also be used to control FHB the most effective fungicide class is the azole fungicide group, specifically prothioconazole, which has the best activity compared to other azoles, followed by metaconazloe and tebuconazole (AHDB, 2017). At present, the understanding is that late-season disease control is not crucial for maximum yield potential being achieved (Bingham et al., 2007a). If the new high yield potential hybrid six-row varieties require increased protection during the grain filling period, coupled with the threat of ramularia and FHB late-season disease control may be a crucial part of the disease management strategy in barley.

Thus, the aim of this study is to investigate, at varying levels of S & N rate, if current fungicide programmes utilised in conventional two-row winter barley varieties need to be altered for six-row varieties, the hypothesis is that due to different yield components that six-row varieties will have a higher requirement for late-season disease control compared to two-row varieties. This was tested through field-based experiments, initially using a conventional two-row and a hybrid six-row variety at two S & N rate programmes, with a range of fungicide programmes applied throughout the season. Subsequently, a conventional six-row and an additional conventional two-row variety were added, while fungicide programmes specifically investigated the requirement for late-season disease control.

2.2 Materials & Methods

2.2.1 Investigating the response to fungicide programmes in a two and six-row variety at two seed and nitrogen rate programmes

A field experiment was established at two sites, Teagasc, Oak Park, Carlow, Ireland and SRUC, Boghall, Edinburgh, Scotland over three seasons 2014/2015 (hereafter 2015), 2015/2016 (2016) and 2016/2017 (2017). Table 2-1 shows the sowing dates, location, soil texture, and previous crop of all six site/season combinations. The experiment was laid out in a split-split plot design with the main plot factor being seed and Nitrogen rate (S & N rate), the split-plot factor being variety, and the split-split plot factor being fungicide programme. Sites were placed in a rotational slot that reflects commercial practice in both countries, and plots were established following inversion ploughing and harrowing. The seed was treated with Redigo Deter ® (50 g l^{-1} prothioconazole and 250 g l^{-1} clothianidin, Bayer Crop Science, Monhem am Rhein, Germany) to prevent barley yellow dwarf virus infection (BYDV). Sowing dates were typical of commercial practice for winter barley in both countries (late September-early October). At each site, treatments were replicated four times with a plot size of 2.5 x 12m. Other nutrients (P, K, and S) were applied at rates not to limit crop growth and development, in accordance with the guidance in Ireland and Scotland (Wall and Plunkett, 2016, Sinclair et al., 2013, Sinclair and Wale, 2013). Crop inputs are listed in appendix 2. Seasonal meteorological data were obtained from onsite met stations located no more than 2 km from each experiment. Long term averages and seasonal values were obtained from the same met station for Teagasc, whereas long-term data for the site at

SRUC was obtained from a met station >6km from the experiment as long-term onsite data was not available.

Table 2-1. Sowing date, latitude/longitude, soil texture, and a rotational slot for both experimental sites. Teagasc, Oak Park, Carlow, Ireland (Teagasc) and SRUC, Boghall farm, Edinburgh, Scotland (SRUC)

Site/season	Sowing date	Latitude, Longitude	Soil texture	Previous Crop
Teagasc 2015	1-Oct	52° 51' N, 6°54' W	loam	Winter wheat
Teagasc 2016	31-Sept	52° 51' N, 6°55' W	loam	Winter wheat
Teagasc 2017	1-Oct	52° 51' N, 6°55' W	loam	Winter wheat
SRUC 2015	18- Sept	55° 52' N, 3°12' W	Medium	Spring Barley
SRUC 2016	18-Sept	55° 52' N, 3°12' W	Medium	Spring Barley
SRUC 2017	16-Sept	55° 52' N, 3°12' W	Medium	Spring Barley

Treatments

S & N rate was the main plot factor, the rates for both inputs are listed in Table 2-2. The rates used were a 'standard' rate of both inputs for each variety, and then these rates were increased by 25%. This was done in an attempt to increase sink capacity through an increase in grain number.m^{-2}, in order to test the hypothesis that the requirement for late-seasonal disease control will increase with higher grains m^{-2}. The N fertiliser was applied in two applications, one-third of the total rate at mid to late tillering (growth stage (GS)2 5-29 (Zadoks et al., 1974)) and two thirds at the onset of stem extension (GS30/31)

The split-plot factor was variety, with two varieties used, an F1 hybrid six-row variety, Volume (Syngenta, Basel, Switzerland) and a conventional two-row variety, KWS Tower (KWS UK Ltd, Thriplow, UK). Both varieties were chosen due to their commercial use in both Ireland and Scotland. The seeds m^{-2} rate was different for each variety to reflect the commercial practice of sowing hybrid six-row varieties at a lower rate compared to conventional two-row varieties, to take advantage of early vigorous growth (Anon., 2019).

Table 2-2. Seed rate (seeds m^{-2}) and Nitrogen (kg N ha^{-1}) programmes for each variety.

Variety Type	**Variety**	**Seed Rate**		**Nitrogen**	
		Seeds m^{-2}		**kg N ha^{-1}**	
		Standard	***+25%***	***Standard***	***+25%***
Two-row	**KWS Tower**	360	450	190	230
Six-row	**Volume**	270	360	190	230

Fungicide programme

The fungicide programmes that were used were as follows;

1. Untreated
2. GS 31/2 (1 spray)
3. GS 31/2, 39/45 (2 spray)
4. G.S. 25, 31/2, 39/45 (3 spray)
5. GS 25, 31/2, 39/45, 65 (4 spray)

Fungicides were first mixed with water and then applied to each plot at a rate of 200 l ha^{-1} of water using a hand-held pressurised plot sprayer, using flat fan nozzles at 200 kPa pressure. Fungicides were applied when the crop was dry, no rainfall was forecast, and little or no wind was present. The 3 spray programme was the commercial standard programme, while the 4 spray programme was used to test the need for late-season (grain filling) disease protection. The products used were typical of a commercial spray program. The GS25 timing used 0.4 l ha^{-1} of prothioconazole 250 g $litre^{-1}$ (Proline®, Bayer Crop Science, Monhem am Rhein, Germany) and 0.4 l ha^{-1} of fenpropimorph 750 g $litre^{-1}$ (Corbel®, BASF, Ludwigshafen, Germany). The GS31/2 and GS49 used 1.8 l ha^{-1} of epoxiconazole, 41.6 g $litre^{-1}$, fluxapyroxad 41.6 g $litre^{-1}$ and pyraclostrobin 66.6 g $litre^{-1}$ (Ceriax®, BASF, Ludwigshafen, Germany). The GS65 timing consisted of 0.4 l ha^{-1} prothioconazole g $litre^{-1}$ and 1 l ha^{-1} of chlorothalonil (CTL) 500 g $litre^{-1}$ (Bravo®, Syngenta, Basel, Switzerland).

In field assessments

At each visit to the site from GS59 the crop was inspected for lodging (>45° from vertical) and leaning (5-45° from vertical). When lodging or leaning had occurred, the area affected was scored on a percentage plot basis, then on subsequent visits, another score was carried out if more leaning and lodging had occurred. A pre-harvest straw breakdown assessment (stem failure $1/3^{rd}$ or more up from the base) was also conducted.

Disease assessments

In order to determine the severity of foliar diseases, the proportion of leaf that displayed symptoms of each disease was visually assessed. The foliar diseases assessed were; Rhynchosporium (*Rhynchosporium commune)*, powdery mildew (*Blumeria graminis f. sp. Hordei)*, ramularia (*ramularia collo-cygni)*, net blotch (*pyrenophora teres)*, the spot form

(*P. teres f. maculate*) and the net form (*P. Teres f. teres*), brown rust and septoria nodorum blotch. FHB was assessed at Teagasc in 2016 and 2017 as a portion of the number of grains infected on each individual ear. The disease assessments conducted are listed in Table 2-3. At each assessment, 10 random main shoots were sampled approximately equidistant apart, avoiding the outer two rows and first 0.5m of each plot. The top 3-4 fully expanded leaves were assessed on each shoot, the percentage area which had green tissue was also assessed for the top 3-4 fully expanded leaves at the final assessment at each site/season. If the visual assessment was not carried out, immediately samples were stored in a cold room (4-6 °C) for no more than three days.

Table 2-3.Growth stages (GS) of disease assessments at the six site/seasons.

Site/season	Disease assessment GS		
SRUC 2015	31/32	59	69
SRUC 2016	31	39	73
SRUC 2017	-	49	77
Teagasc 2015	31/32	49	71
Teagasc 2016	31	49	75
Teagasc 2017	-	-	71

Pre-harvest grab sampling

Pre-harvest grab sampling was conducted no more than three days prior to harvest for assessment of grains ear^{-1} at all sites apart from SRUC 2017. Grabs of 10-15 shoots at five random locations within each plot were cut at ground level, pooled together, labelled, placed in plastic bags ears first to minimise material loss during transport to the lab for processing. The number of ears and non-ear bearing shoots were recorded, samples were then separated into ears and straw (leaf and stem). Each fraction was weighed before being dried in a fan assisted oven at 70 °C for 48 hours or to a constant mass. Following drying, dry weight was determined to the nearest 0.01g. Ears were threshed using a HALDRUP LT-21 laboratory thresher (Haldrup GmbH, Ilshofen, Germany) set up to minimise grain loss. Grain was cleaned using a winnower to remove awns and chaff, weighed and mean grain weight (MGW) was determined to the nearest 1 mg using a grain counter (Pfeuffer GmbH, Kitzingen, Germany) to count the number of grains in a sample of known dry weight. The number of grains ear^{-1} was calculated by dividing the total number of grains per each grab sample by the number of ears in each sample.

Yield and Grain Quality

Plots were harvested using a small plot combine. Moisture, hectolitre weight (HTW) and plot weight were obtained using Harvest Mater classic GrainGauge (Juniper Systems, Inc., 1132 W 1700 N, Logan, UT, 84321, USA). Plot yield was corrected to tonnes ha^{-1} at 85% dry matter (t ha^{-1}). A ~1kg grain sample was taken from each plot for assessment of screenings through a 2.5 mm sieve (Glasblaserei, Institute of Fermentation and Biotechnology, Berlin, Germany) and MGW determination nearest 1 mg using a grain counter (Pfeuffer GmbH, Kitzingen, Germany) to count the number of grains in a sample of known dry weight. The number of grains m^{-2} was calculated as combine yield divided by MGW and corrected to 85% dry matter. Ears m^{-2} were calculated as the number of grains m^{-2} divided by grains ear^{-1} obtained from the grab sample data.

Statistical analysis

All statistical analyses were carried out using GenStat (18th Edition, VSN International Ltd., Hemel Hempstead, UK). Normality was checked using a probability of distribution test in GenStat, while homogeneity was checked using bartlett's test.

Bartlett's test for homogeneity was conducted on yield (t ha^{-1}), grains m^{-2}, MGW (mg), Hectolitre weight (HTW) (kg hl^{-1}), screenings, straw breakdown and lodging to assess the suitability of performing a cross-site ANOVA analysis. All tested variables were significant ($p>0.05$), therefore a cross-site ANOVA would not be suitable as the variance was not homogenous across the site/seasons. Each site/season was therefore analysed separately using a split-split plot ANOVA model where effects of S & N rate, variety, fungicide programme and the interactions between the treatments were analysed. Replicate was included in the blocking structure.

For each disease assessment, total disease was averaged across the top three leaf layers for the ten sampled shoots and then used for subsequent statistical analysis. The top three leaf layers were used as three leaf layers was the common number of layers available at each assessment. Where five or more of the ten sampled shoots had completely senesced, the plot was omitted from the analysis. Total disease for each leaf layer and average (top three leaf layers) individual disease were also analysed (data not presented). The data was firstly arcsine transformed in Microsoft Excel® 2010, and then each assessment was analysed individually using a split-split plot ANOVA model where effects of S & N rate, variety, fungicide programme and the interactions between treatments were analysed. Replicate was included in the blocking structure. Back-transformed means are presented. FHB was assessed at Teagasc in both 2016 and 2017, to analyse the effects of treatments on FHB infection fungicide programmes which had not received the GS65 spray (untreated, 1, 2 and 3 spray) were averaged (- head spray) and compared against the 4 spray programme (+ head spray).

As disease can have varying impacts on yield depending on the stage in the crops life cycle, the relationship between average foliar disease infection and yield was investigated using simple linear regression for each individual site and disease assessment combination. In particular site/seasons, there was a significant degree of straw breakdown, simple linear regression was carried out to investigate if straw breakdown correlated with yield.

2.2.2 Investigating the response to late-season disease control in six and two-row varieties

A field experiment was established at two sites in Ireland, Teagasc, Oak Park, Co. Carlow 52° 51' N, 6°54' W (OP) and Kildalton agricultural college, Piltown, Co Kilkenny 52° 20'

N, 7°18’ W (KIL) in the 2017/2018 (hereafter 2018) growing season. The experiment was laid out in a split-plot design with variety as the main plot and fungicide treatment as the sub-plot factor. At each site, a plot size of 2.5m x 12m was used with four replicates of each treatment. The experiment was established following inversion ploughing and harrowing as per the previous experiment on the 30th September and 4th October 2017 for OP and KIL respectively. The previous crop was winter and spring wheat for the OP and KIL sites respectively. A standard seed rate of 360 seeds m^{-2} for all varieties was used for consistency as no benefit/penalty was seen from increasing or decreasing seed rate in the previous experiment. The seed was treated with Redigo Deter ® (50 g l^{-1} prothioconazole and 250 g l^{-1} clothianidin, Bayer Crop Science, Monhem am Rhein, Germany) to prevent barley yellow dwarf virus infection (BYDV). Again for consistency, this experiment received the same plant growth regulation programme as the previous experiment. A Nitrogen (N) rate of 190 kg N ha^{-1} was used at OP and 200 kg N ha^{-1} for KIL in the form of calcium ammonia nitrate. Other nutrients (P, K, and S) were applied at rates not to limit crop growth and development, in accordance with the regulations governing Ireland and Scotland (Wall and Plunkett, 2016, Sinclair et al., 2013, Sinclair and Wale, 2013). All other crop inputs are listed in appendix 2.

Treatments

The main plot was variety, four varieties were used, Volume and Tower as per the previous experiment with the addition of a conventional six-row variety, KWS Kosmos (KWS UK Ltd, Thriplow, UK) and a conventional two-row, KWS Cassia (KWS UK Ltd, Thriplow, UK).

Fungicide treatment was the sub-plot. Six different treatments were used, all treatments received applications at the GS25, and GS31/32 timings as the object of the experiment was to test late-season disease control. As per the previous experiment the GS 25 timing used 0.4 l ha^{-1} of prothioconazole 250 g litre^{-1} (Proline®, Bayer Crop Science, Monhem am Rhein, Germany) and 0.4 l ha^{-1} of fenpropimorph 750 g litre^{-1} (Corbel®, BASF, Ludwigshafen, Germany). The GS31/32 timing used 1.8 l ha^{-1} of epoxiconazole, 41.6 g litre^{-1}, fluxapyroxad 41.6 g litre^{-1} and pyraclostrobin 66.6 g litre^{-1} (Ceriax®, BASF, Ludwigshafen, Germany). Treatments are listed in Table 2-4, including the 2, 3, and 4 spray programme from the previous experiment with three additional treatments 3 spray + CTL, 4 spray + CTL and 4 spray + proline. The 3 spray + CTL, 4 spray + CTL were to test if CTL was included at the

GS49 timing would there be a requirement for an additional application at GS65. The 4 spray + proline treatment was used to test if product choice at GS49 influenced yield and disease control.

Table 2-4. Fungicide programmes for investigating the response of late-season disease control experiment carried out in 2018.

Fungicide programme	GS 49	GS 65
2 spray	-	-
3 spray	Ceriax® 1.8 l ha^{-1}	-
4 spray	Ceriax® 1.8 l ha^{-1}	Proline® 0.4 l ha^{-1} CTL 1.0 l ha^{-1}
3 spray + CTL	Ceriax® 1.8 l ha^{-1} CTL 1.0 l ha^{-1}	-
4 spray + CTL	Ceriax ®1.8 l ha^{-1} CTL 1.0 l ha^{-1}	Proline® 0.4 l ha^{-1} CTL 1.0 l ha^{-1}
4 spray + proline	Proline ® 0.4 l ha^{-1} CTL 1.0 l ha^{-1}	Proline ® 0.4 l ha^{-1} CTL 1.0 l ha^{-1}

In field assessments

In order to determine the severity of foliar diseases, the proportion of leaf that displayed symptoms of each disease was visually assessed. The sampling of shoots for assessment was carried out using the same protocol as the first experiment. A background disease assessment was carried out prior to the application of the GS49 timing, and a full disease assessment was carried out at GS75 at both sites. At each assessment, ten random main shoots were sampled approximately equidistant apart, avoiding the outer two rows and first 0.5m of each plot. The diseases that were assessed were ramularia, Rhynchosporium, spot form of net blotch, and septoria nodorum blotch. The top two fully expanded leaves were assessed on each shoot. The percentage area which had green tissue was also assessed for the top 3 fully expanded leaves.

Prior to harvest, a straw breakdown assessment (stem failure 1/3rd or more up from the base) was conducted at both sites on a percentage plot basis.

Yield

The site at OP was harvested using two combines due to a breakdown, a Sampo 2010 plot combine (Sampo Rosenlew Ltd Konepajanranta 2, PORI FINLAND) and a Claas compact 85 (CLAAS KGaA mbH, Mühlenwinkel 1, 33428 Harsewinkel, Germany). The first 45 plots were harvested using the Sampo on the 9th July 2018 while the remaining 51 plots were harvested using the Claas 3 days later. The K.I.L. site was harvested using a Deutz-Fahr plot combine and an Allegro CX Field P.C. Data Collector to obtain yields. Moisture content and hectolitre weight (HTW) was obtained using DICKEY-JOHN GAC®2100 GI (Auburn, IL, United States). Plot yield was corrected to tonnes ha $^{-1}$ at 85% dry matter. A ~1kg grain sample was taken from each plot for assessment of screenings through a 2.5mm sieve (Glasblaserei, Institute of Fermentation and Biotechnology, Berlin, Germany) and mean grain weight (MGW) was determined to the nearest 1 mg using a grain counter (Pfeuffer GmbH, Kitzingen, Germany) to count the number of grains in a sample of known dry weight.). The number of grains m^{-2} was calculated as combine yield divided by MGW corrected to 85% dry matter.

Statistical analysis

All statistical analyses were carried out using GenStat (18th Edition, VSN International Ltd., Hemel Hempstead, UK). Normality was checked using a probability of distribution test in GenStat, while homogeneity was checked using bartlett's test.

There was an issue with the weighing system on the combine from the KIL site, therefore, yield and grains m^{-2} are only present from the OP site. Firstly to test if the combine used affected the result the effect of combine on yield was analysed using REML as the design was unbalanced. The combine used did not significantly influence yield ($p>0.05$) nor was there an interaction between combine and any of the treatments, therefore, yield, grains m^{-2}, MGW, screenings, and HTW, where available, were analysed separately for each site using a split-plot model with replicate in the blocking structure. Main effects of variety and fungicide treatment were tested along with the interaction between variety and fungicide.

To analyse the effect of treatments on the level of foliar disease infection on percentage green leaf area (GLA) firstly the total disease and GLA for each leaf layer was totalled and then the mean disease for leaves 1 and 2 was calculated. The data was then arcsine transformed in Microsoft Excel® 2010, and then each assessment was analysed individually using a split-plot ANOVA model testing effects of variety, fungicide treatment, and the interaction between them.

Effects of variety, fungicide, and the interaction between variety and fungicide on straw breakdown were analysed using a split-plot ANOVA model. Each site was analysed individually with replicate included in the blocking structure.

2.3 Results

2.3.1 Investigating the response to fungicide programmes in a two and six-row variety at two seed and nitrogen rate programmes

Meteorological data

The growing season for both sites is defined as the period between October and July.

Teagasc

Long term (1981-2010) average total rainfall was 699 mm for the growing season, while average temperature during the same period was 8.9 °C

Total rainfall during the 2015 season at Teagasc was higher than average (732 mm), while the average temperature of 8.7 °C was similar to the long-term average. Total rainfall during the 2016 season was again higher than average (902 mm), although this was mainly caused by an extremely wet month of December in which rainfall was 124% higher than average, while temperature during the season was higher than normal (average temperature = 9.6 °C). The 2017 season was a dry (season rainfall = 528 mm) and warm (average temperature = 9.3 °C) compared to long-term averages.

Cumulative global radiation at Teagasc had a seasonal average of 2698 MJ m^{-2} in the period from 2008-2014. Teagasc 2015 had a more substantial amount of radiation than average (accumulated radiation = 2951 MJ m^{-2}), monthly values for March, April and June were above average values (Figure 2-3). Teagasc 2016 had a similar level of radiation compared to normal (accumulated radiation = 2638 MJ m^{-2}), following a similar trend to average values, although the radiation in May was above normal while radiation in June was lower than average (Figure 2-3). Teagasc 2017 experienced above average radiation for the season (accumulated radiation = 2826 MJ m^{-2}), values for March and May were above average, while values for April were below average (Figure 2-3).

SRUC

SRUC, located further north and at a higher altitude than the Teagasc site, had a higher long-term average total rainfall of 817 mm and a cooler long-term average temperature of 7 °C. The 2015 season had more rainfall and cooler temperatures compared to long-term averages

with total rainfall for the season of 1142 mm and an average temperature of 6.7 °C. The 2016 season was also a wet season (total rainfall = 1267 mm), with the majority of the above average rainfall occurring in the winter months (Figure 2-1), while the temperature was higher than normal (average temperature = 7.6 °C). The 2017 season was dry (total rainfall = 615 mm) with below average rainfall for all months except June (Figure 2-1) and temperature was above long-term average warm (average temperature = 8.2 °C).

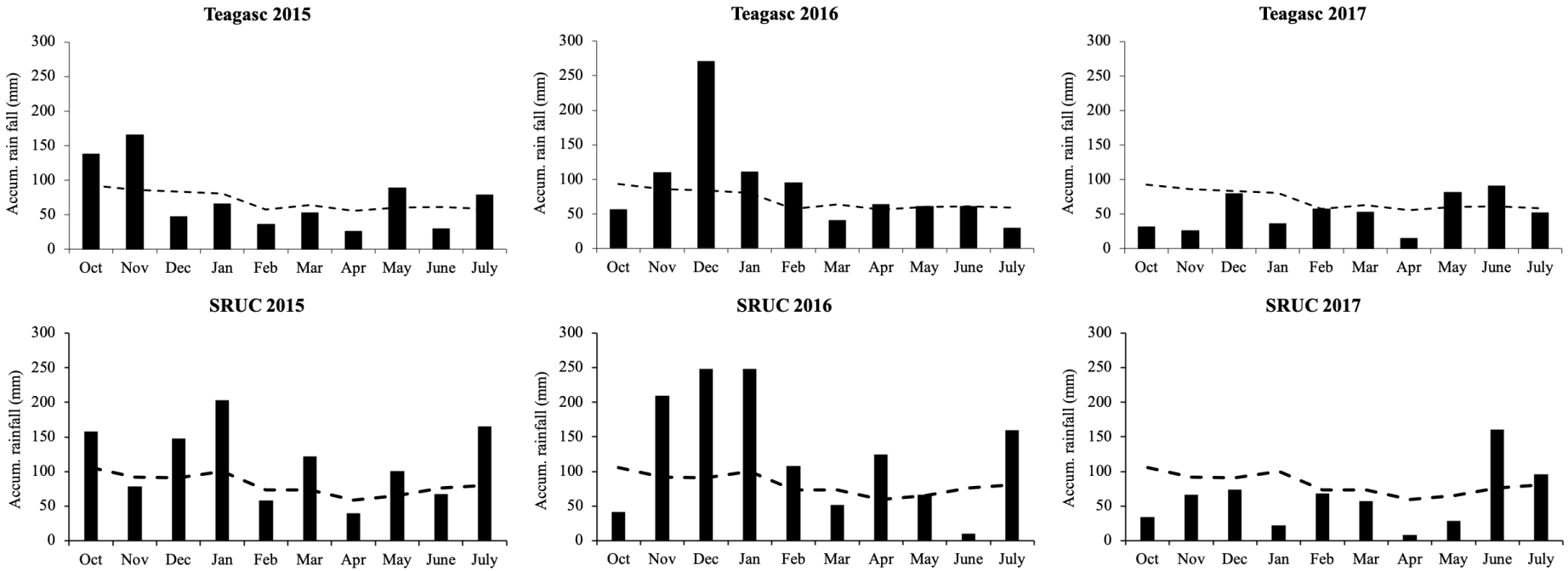

Figure 2-1. Monthly accumulated rainfall (mm) from October to July at all sites/season. Broken line shows long term averages (1981-2010).

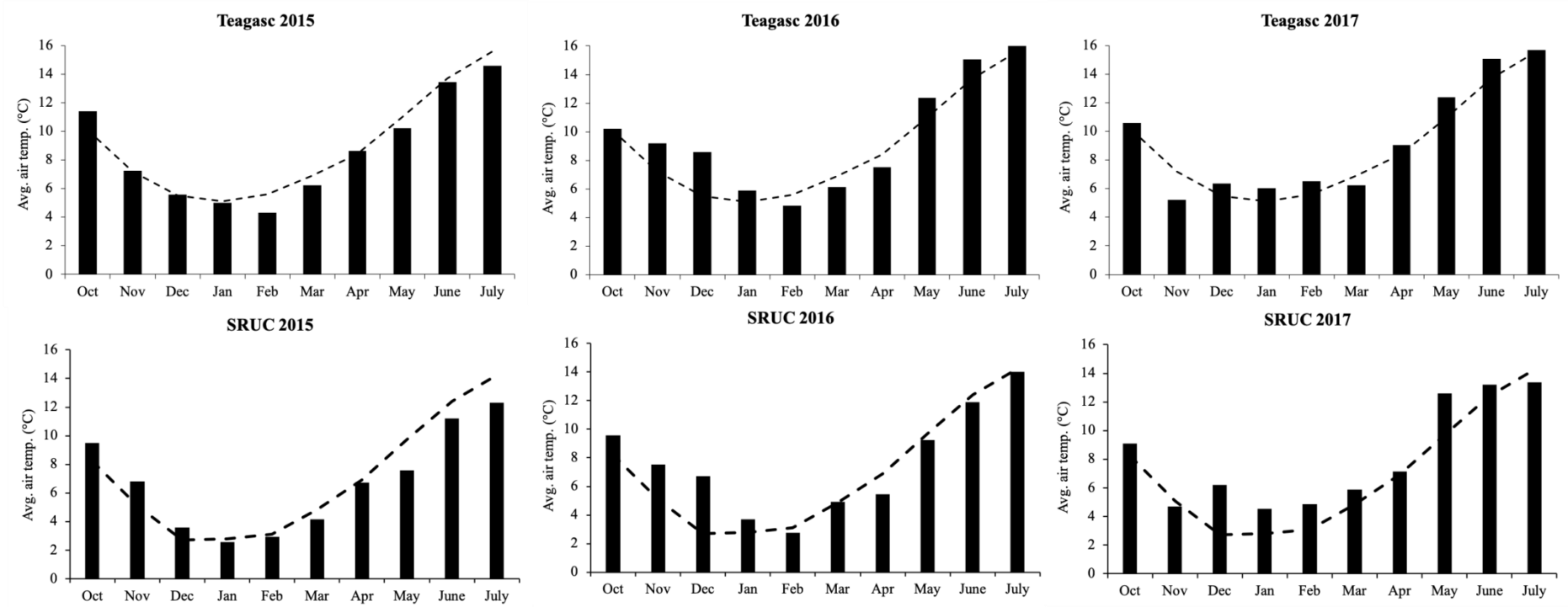

Figure 2-2. Monthly mean temperature (°C) from October to July for all site/seasons. Broken line shows long term averages (1981-2010)

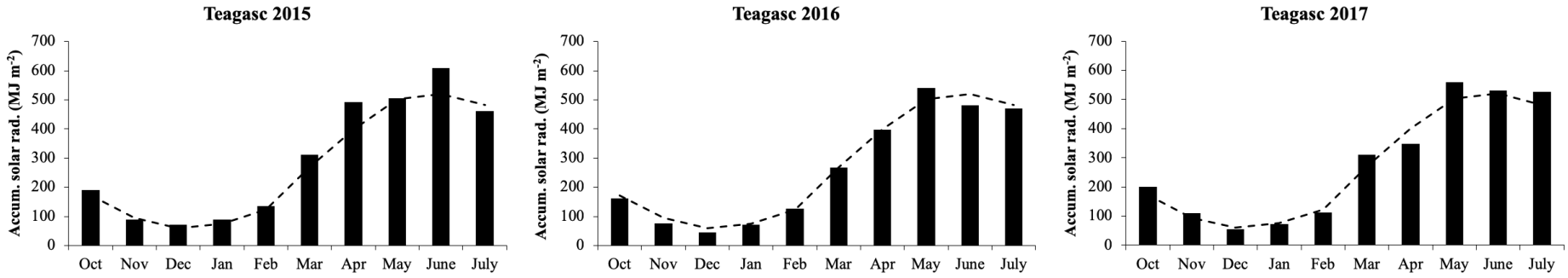

Figure 2-3. Monthly accumulated global radiation (MJ m^{-2}) from October to July. Broken lines show long term average (2008-2014)

Disease

The disease pressure and spectrum observed over the site/season combinations are presented in Table 2-5. At both sites in 2015, the pressure was low, powdery mildew and rhynchosporium dominated the disease spectrum, with some level of brown rust present at the Teagasc site. In the 2016 season, there was moderate disease pressure at the SRUC site but high disease pressure at the Teagasc site. Septoria nodorum dominated early season at the Teagasc site in 2016, with powdery mildew and ramularia developing as the season progressed. Early and mid-season rhynchosporium and powdery mildew again dominated at the SRUC site in 2016, both of these diseases remained present through the season with the addition of rust and net blotch as the season progressed. 2017 was a high disease pressure season at both sites, Ramularia and mildew dominated at the Teagasc site while mildew and net blotch dominated at the SRUC site.

Central to the hypothesis of the study is the interaction between variety and fungicide, of which there were seven significant interactions out of the fifteen assessments conducted for the average disease of the crop ($p<0.05$). Three of the seven significant interactions occurred in late-season disease assessments at SRUC 2016, SRUC 2017 and Teagasc 2017 (Table 2-7, Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 1, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-8 and Table 2-11). These interactions were caused by variance in disease levels in the untreated and 1 spray programmes.

There were, however, differences in how both varieties responded to the remaining fungicide programmes. The significant variety x fungicide interactions at SRUC 2015 at GS31and SRUC 2016 at GS39 was caused by a higher level of disease in the untreated Tower compared to Volume ($p<0.05$), whereas there was no difference when fungicide was applied ($p>0.05$) (Table 2-6 and Table 2-7). The reverse of this was the cause of the interaction at Teagasc 2015 at GS31, where Volume had a higher level of disease in the untreated programme compared to Tower ($p<0.05$) (Table 2-9). The significant variety x fungicide interaction at SRUC 2016 at GS73 was caused by a variance in the response between the untreated treatment and the 1 spray programme, while the varieties responded similarly to the 2, 3, and 4 spray fungicide programmes. There was significantly more disease in the untreated programme in Volume compared to Tower ($p<0.05$), while in Tower there was a significant benefit of the 1 spray programme (GS31/32 timing) compared to the untreated ($p<0.05$), while this was not true for Volume ($p>0.05$) (Table 2-7). Both assessments carried

out at SRUC 2017 had significant variety x fungicide interactions ($p<0.05$), caused by the Volume having a higher level of disease infection in both untreated and 1 spray programme compared to Tower ($p<0.05$), while response to the 2, 3 and 4 spray programme was similar ($p>0.05$). Further to the previously mentioned difference for the 3 spray programme between Tower and Volume at Teagasc 2017 there was also higher levels of disease in the 2 spray programme in Tower compared to Volume ($p<0.05$), while infection was similar for the untreated, 1 spray and 4 spray programmes ($p>0.05$).

Fungicide programme had a significant effect on the level of disease at all assessments conducted ($p<0.05$) except for the GS31 assessment at both sites in 2016. In general fungicide treatment reduced the level of disease compared to the untreated even in the low disease pressure season of 2015 where programmes had significantly lower disease compared to the untreated ($p<0.05$) (Table 2-6, Table 2-9). In higher pressure seasons (2016 & 2017) the reduction in disease from fungicide treatment was also significant compared to the untreated control ($p<0.05$). Early season disease control (GS25 and GS31/32 timings) significantly reduced disease when assessed early ($p<0.05$). The effect of the GS49 timing on foliar disease control can be seen at the final assessment conducted at all sites, there was no significant benefit over the 1 spray programme at either site in 2015 and Teagasc 2016 ($p>0.05$), although at the remaining sites there was a significant benefit over the 1 spray programme to foliar disease control ($p<0.05$). Interestingly at sites where there was high late-season disease pressure (both sites in 2016 & 2017) the addition of the GS65 timing in the 4 spray programme significantly reduced disease levels in both varieties compared to the 3 spray programme ($p<0.05$) with the exception of SRUC 2017 where there was no additional benefit on disease control of the 4 spray programme compared to 3 spray ($p>0.05$).

Of all the assessments carried out, there was no significant difference in disease observed between the two S & N rate programmes ($p>0.05$). There was no consistent trend as to which variety had higher levels of foliar disease across all sites and treatments, although, at individual assessments, there were significant differences between the two varieties. At SRUC in 2015, Tower had significantly higher levels of disease compared to Volume at GS31 and at GS59 ($p<0.05$) (Table 2-6). At the same site in 2016, Tower had higher levels of disease compared to Volume ($p<0.05$), although this was only early in the season, whereas disease levels were significantly higher in Volume compared to Tower at GS73 ($p<0.05$) (Table 2-7). At SRUC in 2017, at both GS49 and GS75 assessments, there were significantly

higher disease levels in Volume compared to Tower ($p<0.05$) (Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 1, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-8). At Teagasc for all assessments carried out over the three seasons, only once was there a statistical difference between the varieties. At GS69 in Teagasc 2015, Volume had a higher level of disease compared to Tower ($p<0.05$) (Table 2-9).

While there was no overall effect of S & N rate on disease levels there was however a significant S & N rate x fungicide programme interaction ($p<0.05$) at SRUC 2015 at GS59 (Table 2-7) caused by a higher level of disease at the higher S & N programme in the untreated programme ($p<0.05$). There were also apparently significant three-way S & N rate x variety x fungicide programme interactions ($p<0.05$) at four assessments (SRUC 2015 GS31, SRUC 2016 GS73, Teagasc 2015 GS31, Teagasc 2016 GS75) but these appeared to be due to variation in disease in untreated plots.

Fusarium head blight (FHB) was assessed at two site/seasons Teagasc 2016 and 2017 (Table 2-12). While there were main effects of S & N rate, Variety and fungicide programme, the interaction between variety and fungicide was not significant in either assessment ($p>0.05$). At Teagasc 2016 there were significantly higher levels of FHB present at the higher S & N rate compared to the standard rate ($p<0.05$), no difference was observed in 2017 ($p>0.05$). There was significantly less infection in Tower compared to Volume ($p<0.05$), again in 2016 only. Fungicide programme had a significant effect on the level of FHB, all programmes receiving the GS65 application having less infection compared to those that did not ($p<0.05$) in both 2016 and 2017. There were no significant two or three-way interactions ($p>0.05$).

Table 2-5. Disease pressure observed from the six site/season combinations. Values presented are back-transformed means of both S & N rate programmes and varieties from untreated plots only of individual disease levels averaged across the top three leaves at each assessment.

Site/season	GS	RHY	RAM	SN	MILD	RUST	NB	FHB
SRUC 2015	31	0.2	0.0	0.0	0.6	0.0	0.0	-
	59	0.4	0.0	0.0	0.4	0.0	0.0	-
	69	0.1	0.0	0.0	0.4	0.0	0.0	-
SRUC 2016	31	1.0	0.0	0.0	0.4	0.0	0.5	-
	39	0.2	0.0	0.0	0.1	0.0	0.0	-
	63	0.6	0.0	0.0	6.7	0.1	1.2	-
	73	0.3	0.0	0.0	4.0	2.2	1.3	-
SRUC 2017	49	0.0	0.0	0.0	3.8	0.0	0.0	-
	77	0.0	0.0	0.0	12.9	0.1	3.9	-
Teagasc 2015	31	0.1	0.0	0.0	0.3	0.9	0.0	-
	49	2.0	0.0	0.0	0.1	2.1	0.0	-
	69	0.1	0.0	0.0	3.3	0.0	0.0	-
Teagasc 2016	31	0.0	0.0	2.5	0.3	0.2	0.0	-
	49	0.2	0.0	0.8	6.7	0.1	0.0	-
	75	0.0	22.3	0.0	2.0	1.1	0.0	14.5
Teagasc 2017	75	0.0	8.2	0.0	17.0	0.3	0.0	6.2

GS = Growth stage, RHY = % Rhynchosporium, RAM = % Ramularia, SN = % Septoria Nodorum, MILD = % Powdery Mildew, RUST = % brown rust, NB = % net blotch, FHB = % Fusarium head blight

Table 2-6. The effect of treatments in SRUC 2015 on the average disease and green leaf area on the top three leaf layers. P Values and means (back-transformed) were produced from a split-split plot ANOVA analysis

SRUC 2015						
			GS31	GS49	GS65	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	1.8	1.7	3.4	90.5
		1	0.0	0.2	0.3	95.9
		2	0.0	0.1	0.1	95.9
		3	0.3	0.1	0.3	95.7
		4	0.0	0.1	0.0	96.1
	Mean		**0.4**	**0.4**	**0.8**	**94.8**
High	Volume	unt	1.1	1.2	4.1	90.6
		1	0.0	0.3	0.6	95.8
		2	0.0	0.1	0.2	96.1
		3	0.1	0.2	0.1	95.3
		4	0.0	0.0	0.2	95.1
	Mean		**0.2**	**0.4**	**1.1**	**94.6**
Standard	Tower	unt	1.7	0.4	1.5	94.8
		1	0.0	0.0	0.4	96.0
		2	0.0	0.1	0.0	95.6
		3	0.1	0.0	0.1	94.3
		4	0.0	0.1	0.1	96.7
	Mean		**0.4**	**0.1**	**0.4**	**95.5**
Standard	Volume	unt	0.6	0.4	1.7	94.1
		1	0.0	0.1	0.3	96.3
		2	0.0	0.0	0.2	95.9
		3	0.3	0.0	0.0	96.5
		4	0.0	0.0	0.0	96.2
	Mean		**0.2**	**0.1**	**0.4**	**95.8**
Significance		**d.f.**	**P**	**P**	**P**	**P**
S & N rate (S&N)		**1**	0.45	0.013	0.092	0.138
Variety (V)		**1**	0.063	0.674	0.613	0.903
Fungicide (F)		**4**	<.001	<.001	<.001	<.001
S&N*V		**1**	0.902	0.816	0.594	0.4
S&N*F		**4**	0.131	0.017	0.383	0.069
V*F		**4**	0.021	0.384	0.855	0.752
S&N*V*F		**4**	0.041	0.906	0.905	0.776

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-7. The effect of treatments at SRUC 2016 on the average disease and green leaf area on the top three leaf layers. P Values, and means (back-transformed) were produced from a split-split plot ANOVA analysis

SRUC 2016						
			GS31	GS39	GS73	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	3.2	2.6	10.1	57.3
		1	0.0	0.2	5.6	74.3
		2	0.0	0.5	1.8	86.3
		3	1.8	0.1	0.8	87.3
		4	0.0	0.1	0.5	93.0
	Mean		**1.0**	**0.7**	**3.7**	**79.6**
High	Volume	unt	2.5	0.6	8.6	37.4
		1	0.0	0.4	13.6	57.2
		2	0.0	0.1	3.0	73.4
		3	1.7	0.5	5.0	77.1
		4	0.0	0.4	0.7	86.8
	Mean		**0.8**	**0.4**	**6.2**	**66.4**
Standard	Tower	unt	5.1	3.3	5.7	53.9
		1	0.0	0.5	4.1	72.9
		2	0.0	0.2	0.6	82.4
		3	4.3	0.1	1.6	83.8
		4	0.0	0.3	0.1	94.9
	Mean		**1.9**	**0.9**	**2.4**	**77.6**
Standard	Volume	unt	2.8	0.4	15.8	35.0
		1	0.0	0.4	11.1	61.2
		2	0.0	0.4	1.6	82.8
		3	1.9	0.7	0.9	88.1
		4	0.0	0.2	0.1	94.1
	Mean		**0.9**	**0.4**	**5.9**	**72.2**
Significance		d.f.	P	P	P	P
S & N rate (S&N)		1	0.149	0.172	0.205	0.406
Variety (V)		1	0.009	0.147	0.004	<.001
Fungicide (F)		4	0.083	<.001	<.001	<.001
S&N*V		1	0.057	0.596	0.814	0.006
S&N*F		4	0.666	0.986	0.478	0.225
V*F		4	0.942	<.001	0.04	0.008
S&N*V*F		4	0.667	0.166	0.002	0.281

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 1, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-8. The effect of treatments at SRUC 2017 on the average disease and green leaf area on the top three leaf layers. P Values and means (back-transformed) were produced from a split-split plot ANOVA analysis

SRUC 2017					
			GS49	GS77	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg GLA
High	Tower	unt	2.8	16.2	63.0
		1	0.6	5.3	80.3
		2	1.8	0.4	85.1
		3	2.4	0.0	84.4
		4	1.6	0.6	78.7
	Mean		**1.8**	**4.5**	**78.3**
High	Volume	unt	6.3	24.9	63.3
		1	3.1	11.8	77.1
		2	1.1	1.8	81.6
		3	1.3	0.5	81.4
		4	0.9	0.1	83.0
	Mean		**2.5**	**7.8**	**77.3**
Standard	Tower	unt	1.3	14.7	69.3
		1	1.3	3.6	82.6
		2	1.0	0.9	87.9
		3	1.9	0.4	85.5
		4	1.9	0.0	89.8
	Mean		**1.5**	**3.9**	**83.0**
Standard	Volume	unt	6.6	16.8	71.4
		1	2.4	10.0	79.8
		2	1.6	0.6	83.0
		3	1.6	0.3	85.3
		4	1.3	0.1	87.6
	Mean		**2.7**	**5.6**	**81.4**
Significance		d.f.	P	P	P
S & N rate (S&N)		1	0.887	0.163	0.006
Variety (V)		1	0.013	0.026	0.363
Fungicide (F)		4	<.001	<.001	<.001
S&N*V		1	0.252	0.326	0.795
S&N*F		4	0.829	0.188	0.318
V*F		4	<.001	<.001	0.487
S&N*V*F		4	0.46	0.116	0.683

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-9. The effect of treatments at Teagasc 2015 on the average disease and green leaf area on the top three leaf layers. P Values and means (back-transformed) were produced from a split-split plot ANOVA analysis.

			Teagasc 2015			
			GS31	GS49	GS65	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	1.5	4.2	3.1	70.2
		1	0.0	1.0	0.5	92.7
		2	0.0	0.0	0.3	91.3
		3	0.1	0.6	0.1	90.9
		4	0.0	0.0	0.0	93.7
	Mean		**0.3**	**1.2**	**0.8**	**87.8**
High	Volume	unt	2.1	3.5	6.0	69.2
		1	0.0	1.0	1.3	86.1
		2	0.0	0.0	0.5	93.5
		3	0.3	0.6	0.4	92.6
		4	0.0	0.0	0.4	92.7
	Mean		**0.5**	**1.0**	**1.7**	**86.8**
Standard	Tower	unt	0.6	3.9	2.4	71.9
		1	0.0	0.5	0.8	84.0
		2	0.0	0.0	0.3	86.2
		3	0.2	0.3	0.2	92.4
		4	0.0	0.0	0.2	94.9
	Mean		**0.2**	**0.9**	**0.8**	**85.9**
Standard	Volume	unt	1.8	5.5	3.5	72.0
		1	0.0	0.9	1.0	85.5
		2	0.0	0.0	0.3	89.6
		3	0.1	0.7	0.5	91.2
		4	0.0	0.0	0.4	90.6
	Mean		**0.4**	**1.4**	**1.1**	**85.8**
Significance		**d.f.**	**P**	**P**	**P**	**P**
S & N rate (S&N)		**1**	0.238	0.93	0.847	0.562
Variety (V)		**1**	0.064	0.51	0.005	0.512
Fungicide (F)		**4**	<.001	<.001	<.001	<.001
S&N*V		**1**	0.952	0.315	0.128	0.814
S&N*F		**4**	0.082	0.516	0.254	0.26
V*F		**4**	0.034	0.999	0.563	0.397
S&N*V*F		**4**	0.02	0.864	0.976	0.436

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-10. The effect of treatments at Teagasc 2016 on the average disease and green leaf area on the top three leaf layers. P Values and means (back-transformed) were produced from a split-split plot ANOVA analysis

Teagasc 2016						
			GS31	GS39	GS73	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	4.9	3.0	31.8	0.0
		1	0.0	1.0	32.8	12.2
		2	0.0	1.1	32.3	22.5
		3	4.2	0.6	26.0	19.8
		4	0.0	0.8	11.5	41.7
	Mean		**1.8**	**1.3**	**26.9**	**19.3**
High	Volume	unt	5.4	4.4	30.4	2.7
		1	0.0	1.1	24.8	11.0
		2	0.0	1.2	26.1	21.4
		3	3.9	1.0	31.1	23.1
		4	0.0	0.8	17.1	37.9
	Mean		**1.9**	**1.7**	**25.9**	**19.2**
Standard	Tower	unt	4.9	4.4	32.5	9.0
		1	0.0	0.9	27.9	12.6
		2	0.0	1.0	25.3	16.7
		3	3.5	0.8	31.8	23.2
		4	0.0	0.9	10.6	55.1
	Mean		**1.7**	**1.6**	**25.6**	**23.3**
Standard	Volume	unt	4.4	3.7	30.0	15.3
		1	0.0	0.8	35.2	14.5
		2	0.0	1.1	22.3	28.2
		3	2.7	0.7	25.3	22.9
		4	0.0	1.1	9.8	51.4
	Mean		**1.4**	**1.5**	**24.5**	**26.5**
Significance		d.f.	P	P	P	P
S & N rate (S&N)		1	0.149	0.172	0.205	0.406
Variety (V)		1	0.009	0.147	0.004	<.001
Fungicide (F)		4	0.083	<.001	<.001	<.001
S&N*V		1	0.057	0.596	0.814	0.006
S&N*F		4	0.666	0.986	0.478	0.225
V*F		4	0.942	<.001	0.04	0.008
S&N*V*F		4	0.667	0.166	0.002	0.281

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-11. The effect of treatments in Teagasc 2017 on the average disease and green leaf area on the top three leaf layers. P Values and means (back-transformed) were produced from a split-split plot ANOVA analysis.

Teagasc 2017				
			GS75	
S & N rate	**Variety**	**Fungicide**	**Avg dis**	**Avg GLA**
High	**Tower**	**unt**	24.6	5.1
		1	23.4	30.3
		2	9.3	53.6
		3	9.2	57.3
		4	0.6	85.5
	Mean		**13.4**	**46.4**
High	**Volume**	**unt**	32.8	24.9
		1	19.9	46.4
		2	4.9	75.6
		3	3.1	81.1
		4	0.8	89.8
	Mean		**12.3**	**63.6**
Standard	**Tower**	**unt**	24.6	34.7
		1	17.9	30.1
		2	9.1	52.4
		3	8.4	57.7
		4	0.1	95.6
	Mean		**12.0**	**54.1**
Standard	**Volume**	**unt**	18.9	55.9
		1	12.4	61.9
		2	4.4	79.5
		3	2.6	78.2
		4	0.3	95.3
	Mean		**7.7**	**74.2**
Significance		**d.f.**	P	P
S & N rate (S&N)		**1**	0.127	0.094
Variety (V)		**1**	0.054	0.004
Fungicide (F)		**4**	<.001	<.001
S&N*V		**1**	0.388	0.958
S&N*F		**4**	0.355	<.001
V*F		**4**	0.013	0.015
S&N*V*F		**4**	0.402	0.467

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-12. The effect of GS65 timing on the Fusarium infection (back-transformed) occurred at Teagasc 2016 & 2017. P Values and means were produced from a split-split plot ANOVA analysis. "+" treatments are the 4 spray programme, "-" treatments are a combination of untreated, 1, 2 and 3 spray programmes.

S & N rate	Variety	Head spray	Teagasc 2016	Teagasc 2017
High	**Tower**	+	6.5	2.4
High	**Tower**	-	10.1	3.8
	Mean		**8.3**	**3.1**
High	**Volume**	+	12.1	2.0
High	**Volume**	-	21.1	4.0
	Mean		**16.6**	**3.0**
Standard	**Tower**	+	4.3	1.2
Standard	**Tower**	-	9.0	4.3
	Mean		**6.6**	**2.8**
Standard	**Volume**	+	5.8	2.1
Standard	**Volume**	-	16.9	4.9
	Mean		**11.3**	**3.5**
Significance			P	P
S & N rate (S&N)	**1**		0.017	0.149
Variety (V)	**1**		<.001	0.312
Fungicide (F)	**4**		<.001	<.001
S&N*V	**1**		0.247	0.357
S&N*F	**4**		0.215	0.207
V*F	**4**		0.061	0.968
S&N*V*F	**4**		0.659	0.468

The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Yield

Only at one of the six site/season (Teagasc 2017) was the interaction between variety and fungicide significant ($p<0.05$), caused by the untreated programme in Tower having a significantly lower yield than Volume ($p<0.05$) (Table 2-18). When the untreated programme was removed from this analysis, the variety x fungicide interaction was not significant ($p>0.05$). At all site/seasons there was a significant effect of fungicide programme on yield ($p<0.05$), the trend being an increase in yield as more fungicide timings were applied. Early season application of fungicide at GS25 had a positive impact on yield at SRUC 2015 in both varieties and Teagasc 2017 in Tower only ($p<0.05$) due to the low untreated yield, while no benefit of the 3 spray programme over the 2 spray programme was observed at other site/seasons ($p>0.05$). The application of fungicide at GS31/32 in the 1 spray programme led to an increase in yield in all site/season combinations compared to the untreated programme ($p<0.05$). Further increases in yield from the application of fungicide at GS49 occurred at Teagasc 2016 and Teagasc 2017 ($p<0.05$), although at Teagasc 2017 the increase was only observed in Volume. The application of fungicide at GS65 in the 4 spray programme significantly increased yield compared to the 3 spray programme at SRUC 2016 & 2017, Teagasc 2016 and Teagasc 2017 although in Volume only ($p<0.05$).

At no site/season was there a significant effect of increasing S & N rate on yield. However, differences between varieties averaged across all treatments were observed, Tower produced a higher yield than Volume at SRUC 2016 and Teagasc 2015 ($p<0.05$) while Volume produced a significantly higher yield than Tower at SRUC 2017 ($p<0.05$). There was no difference between the varieties at the other site/seasons ($p>0.05$).

A significant S & N rate x variety interaction ($p<0.05$) occurred at SRUC in 2015, caused by yield increasing with an increase in S & N rate in Tower and decreasing in Volume (Table 2-13). At one site/season (Teagasc 2015) there was a significant S & N rate x fungicide interaction caused by a lower yield for the untreated programme at the higher S & N rate compared to the standard rate ($p<0.05$), while the other programmes did not differ with S & N rate ($p>0.05$) (Table 2-16). At SRUC 2017, there was an apparent significant S & N rate x variety x fungicide programme interaction ($p<0.05$), which appears to be due to variation in untreated yield (Table 2-15).

Yield relationship with disease and GLA

Simple linear regression was used to investigate the relationship between yield and both the average level of disease on the top three leaf layers and green leaf area with results shown in Table 2-19. There was a significant relationship between yield and average disease ($p<0.05$) for 13 out of the 15 assessment, but the variance accounted for was low ranging from 0.07 to 0.46. At all assessment of GLA, the relationship with yield was significant ($p<0.05$), with the variance accounted for ranging from 0.17 to 0.58.

Yield components

Mean grain weight (MGW)

At two out of six site/seasons (Teagasc 2016 and SRUC 2017) there was a significant variety x fungicide programme interaction ($p<0.05$), caused by the magnitude of the positive response to MGW observed from fungicide treatment, with Tower showing a larger response than Volume (Table 2-15 and Table 2-17). At both sites/seasons where the interaction was significant, it must be noted the addition of GS65 timing in the 4 spray programme did not significantly increase MGW compared to the 3 spray programme in either Volume or Tower ($p>0.05$). The interaction at Teagasc 2016 was caused by a variance in response to the 1 spray programmes (Table 2-17). Application at GS31/32 did not increase MGW significantly compared to the untreated in Volume whereas the increase was significant in Tower ($p<0.05$). In both varieties, programmes that received fungicide at GS49 (2, 3 and 4 spray programmes) had similar MGW ($p>0.05$) and were significantly higher than treatments which did not receive fungicide at GS49 (untreated and 1 spray). At SRUC 2017 application of fungicide at GS31 significantly increased MGW compared to the untreated programme in both varieties , while in Volume there was no further significant increase in MGW from the remaining programmes ($p>0.05$), however in Tower the 3 and 4 spray programmes MGW was significantly higher than the untreated and 1 spray programme but not the 2 spray (Table 2-15).

Fungicide programme significantly affected MGW at all site/season ($p<0.05$), In general, the trend was an increase in MGW with fungicide treatment, with the untreated programme producing the lowest MGW at all site/seasons. The benefit of fungicide treatment on MGW was observed even in the low disease pressure site/seasons (both sites in 2015), where there

was a significant benefit on MGW of all fungicide programmes compared to the untreated ($p<0.05$).

Only at one out of the six site/seasons (SRUC 2017) was there a significant difference in the MGW observed between the S & N rates ($p<0.05$), the standard rate producing a higher MGW compared to the higher rate (Table 2-15), while no statistical difference was seen at the other sites ($p>0.05$). At all site/seasons, Volume had a significantly lower MGW compared to Tower ($p<0.05$). SRUC 2015 was the only site where a significant S & N rate x variety interaction was observed ($p<0.05$), caused by MGW increasing with an increase in S & N rate in Tower while in Volume MGW decreased with an increase in S & N rate ($p<0.05$) (Table 2-13).

Grains m^{-2}

At three out of the six site/seasons (SRUC 2017 and Teagasc 2015 & 2016) significant variety x fungicide programme interactions ($p<0.05$) occurred, caused by a difference in the magnitude of increase in grains m^{-2} from the application of fungicide, with Volume displaying a larger grains m^{-2} response compared to Tower. Interestingly differences in how grains m^{-2} in both varieties responded to the 3 and 4 spray programmes differed at two sites/seasons SRUC 2017 and Teagasc 2016, there was a significant increase in grains m^{-2} in the 4 spray compared to the 3 spray programme in Volume only, with similar grains m^{-2} in the two programmes observed in Tower (Table 2-15 and Table 2-17). The variety x fungicide interaction at SRUC 2017 was not only caused by a variance in response to the 3 and 4 spray programmes. In Tower programmes that received fungicide did not differ from each other ($p>0.05$), while in Volume there was a significant difference between the 2 and 1 spray programmes (GS49 application) while the addition of the GS25 (3 v 2 spray) and GS31/32 (untreated v 1 spray) timing did not increase grains m^{-2} significantly ($p<0.05$). At Teagasc 2015 in Volume, all programmes which received fungicide produced significantly higher grains m^{-2} compared to the untreated ($p<0.05$) while in Tower the 3 spray programme was the only programme in which grains m^{-2} were significantly higher than the untreated programme (Table 2-16). At Teagasc 2016 the interaction was not solely caused by the above-mentioned variance in response to the 2 and 3 spray programmes. The response to the 1 and 3 spray programmes (GS31/32 and GS25) were similar in both varieties while the

response to the 2 spray varied, with grains m^{-2} increasing significantly in Volume and not in Tower when compared with the 1 spray programme (Table 2-17).

Like MGW at all site/seasons, fungicide programme had a significant influence on the grains m^{-2} ($p<0.05$), with the trend being an increase in grains m^{-2} with fungicide treatment.

There was no significant difference observed in grains m^{-2} between the two S & N rates when averaged across all treatments at any of the site/season combinations ($p>0.05$), while Volume produced significantly more grains m^{-2} compared to Tower at all site/seasons ($p<0.05$).

Interestingly there was a significant S & N rate x fungicide programme interaction ($p<0.05$) at Teagasc 2015, this was caused by a significant increase in grains m^{-2} from fungicide treatment compared to the untreated programme observed at the higher S & N rate ($p<0.05$), while there was no difference observed at the standard rate ($p>0.05$).

Ears m^{-2}

Only at one out of the five site/seasons (Teagasc 2017) did ears m^{-2} respond differently to fungicide treatment, in the two varieties with the interaction being caused by fungicide treatment increasing ears m^{-2} to a larger extent in Tower compared to Volume (Table 2-18). A significant main effect of fungicide programme only occurred at one other site/season (Teagasc 2015), where the 2 and 3 spray programmes were the only programmes to increase ears m^{-2} significantly compared to the untreated programme ($p<0.05$) (Table 2-16).

At no site/season did S & N rate significantly affect the ears m^{-2} observed ($p<0.05$). At all site/season where ears m^{-2} were measured, Tower had significantly more ears m^{-2} compared to Volume ($p<0.05$). There was a significant two way S & N rate x variety interaction at Teagasc 2017 ($p<0.05$) caused by increasing S & N rate significantly increasing ears m^{-2} in Volume only, while no significant difference occurred in Tower (Table 2-18). There were no other significant two or three-way interactions at the remaining site/season ($p>0.05$).

Grains ear^{-1}

At two out of the five site/season where grains ear^{-1} were measured, there was a significant variety x fungicide interaction ($p<0.05$). These interactions were caused by grains ear^{-1} in Tower showing no response to fungicide programmes while in Volume there was a significant response to fungicide treatment. Interestingly in Volume grains, ear^{-1} was

significantly increased comparing the 3 and 4 spray programmes at both sites ($p<0.05$), while at SRUC 2016 further to the mentioned difference between the 3 and 4 spray programmes grains ear^{-1} in the 1 and 2 spray programmes were significantly higher than the untreated. The difference between the 3 and 4 spray programme was the only difference observed at Teagasc 2017 with all other programmes being similar (Table 2-14 and Table 2-18). The only other site where fungicide affected grains ear^{-1} was Teagasc 2016 where the 2 and 4 spray programmes were the only treatment to increase the number of grains ear^{-1} significantly compared to the untreated programme ($p<0.05$) (Table 2-17).

Teagasc 2015 was the only site/season that the high S & N rate had significantly higher grains ear^{-1} compared to the standard rate ($p>0.05$), no difference between rates was observed at the remaining site/seasons ($p>0.05$) (Table 2-16). At all site/seasons where grains ear^{-1} was measured Volume had a significantly higher number of grains ear^{-1} compared to Tower ($p<0.05$). A significant S & N rate x variety interaction occurred at Teagasc 2017, caused by grains ear^{-1} a significantly increasing with S & N rate in Volume ($p<0.05$) while no significant effect was observed in Tower ($p>0.05$) (Table 2-18).

Grain quality

Hectolitre weight

Only at one out of six sites/season (Teagasc 2017) was there a significant variety x fungicide interaction caused by a larger increase in HTW in Tower compared to Volume, although the difference between the HTW observed for the 3, and 4 spray programmes was not significant for either variety ($p>0.05$) (Table 2-25). Fungicide programme significantly impacted on HTW at all site/seasons except SRUC 2016, the trend is an increase in HTW with fungicide treatment, with the untreated programme producing the lowest HTW.

SRUC 2015 was the only site/season where a significant effect of S & N rate was observed on HTW, the higher rate producing a significantly higher HTW compared to the standard rate ($p<0.05$). Volume had significantly lower HTW compared to Tower at both SRUC 2015 and Teagasc 2015 & 2016 ($p<0.05$) while no difference was observed at the other site/seasons ($p>0.05$). There was also a significant S & N rate x fungicide interaction ($p<0.05$) at SRUC 2015, caused by the 4 spray programme being the only treatment having

a higher HTW compared to the untreated at the standard rate, while at the high rate all programmes had a higher HTW compared to the untreated (Table 2-20).

Screenings

There was a significant variety x fungicide programme interaction ($p<0.05$) at two site/seasons (Teagasc 2015 & 2017), caused by higher screenings observed in untreated Volume compared to Tower ($p>0.05$) (Table 2-23, Table 2-25).

Teagasc 2017 was the only site/season where a significant effect of S & N rate was observed on the level of screenings, caused by a higher level of screenings at the higher rate compared to the standard rate ($p<0.05$). At all site/seasons with the exception of SRUC 2016, there were significantly more screenings observed in Volume compared to Tower ($p<0.05$).

Significant S & N rate x variety interactions occurred at SRUC 2017, and Teagasc 2016, caused by increasing S & N rate does not affect the level of screenings in Tower ($P>0.05$) while screenings were significantly increased in Volume. There were a significant S & N rate x fungicide programme interaction and significant three-way S & N rate x variety x fungicide programme ($p<0.05$) was observed at Teagasc 2015 by very high screenings in high seed rate, untreated Volume (Table 2-20)

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Table 2-13. Effects of treatments on the yield and yield components for SRUC 2015. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

SRUC 2015							
S & N rate	**Variety**	**Fungicide**	**Yield t ha^{-1}**	**Grains m^{-2}**	**MGW (mg)**	**Ears m^{-2}**	**Grains ear^{-1}**
High	**Tower**	**unt**	10.9	20109	54.4	1194	18.1
		1	11.6	19869	58.6	1175	17.5
		2	11.9	20545	58.1	1283	16.4
		3	12.7	21624	58.8	1289	16.8
		4	12.6	21639	58.5	1246	17.5
	Mean		**12.0**	**20757**	**57.6**	**1237**	**17.3**
High	**Volume**	**unt**	10.6	30347	34.8	789	39.1
		1	11.6	31694	36.7	872	36.3
		2	12.0	31649	38.1	925	34.6
		3	12.3	33197	37.0	940	36.1
		4	12.6	31739	39.7	918	36.3
	Mean		**11.8**	**31725**	**37.2**	**889**	**36.5**
Standard	**Tower**	**unt**	10.7	19536	54.7	1202	16.3
		1	11.4	20552	55.2	1210	16.8
		2	11.4	20289	56.1	1225	16.8
		3	11.6	21223	54.8	1283	17.0
		4	12.2	21068	57.8	1255	16.9
	Mean		**11.4**	**20534**	**55.7**	**1235**	**16.8**
Standard	**Volume**	**unt**	11.0	29607	37.3	830	35.8
		1	12.1	32076	37.9	920	35.0
		2	11.7	30847	38.3	940	34.2
		3	12.3	31757	38.7	972	32.8
		4	12.8	32638	39.3	898	36.4
	Mean		**12.0**	**31385**	**38.3**	**912**	**34.8**

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	**1**	0.581	ns	0.749	ns	0.563	ns	0.871	ns	0.390	ns
Variety (V)	**1**	0.173	ns	<0.001	1161	<0.001	1.4	<0.001	116	<0.001	2.3
Fungicide (F)	**4**	<0.001	0.3	<0.001	791	<0.001	1.2	0.211	ns	0.709	ns
S&N*V	**1**	0.037	0.8	0.906	ns	0.042	2.2	0.799	ns	0.570	ns
S&N*F	**4**	0.058	0.8	0.327	ns	0.191	ns	0.978	ns	0.904	ns
V*F	**4**	0.666	ns	0.437	ns	0.899	ns	0.930	ns	0.887	ns
S&N*V*F	**4**	0.654	ns	0.578	ns	0.181	ns	0.992	ns	0.967	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-14. Effects of treatments on the yield and yield components for SRUC 2016. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

			SRUC 2016				
S & N rate	**Variety**	**Fungicide**	**Yield t ha^{-1}**	**Grains m^{-2}**	**MGW (mg)**	**Ears m^{-2}**	**Grains ear^{-1}**
High	**Tower**	**unt**	6.3	12299	50.8	860	14.6
		1	7.1	12656	56.5	939	13.5
		2	8.3	14532	57.2	908	16.1
		3	8.5	14963	57.5	883	17.3
		4	8.6	14598	58.8	775	18.7
	Mean		**7.8**	**13810**	**56.2**	**873**	**16.0**
High	**Volume**	**unt**	6.4	16553	38.8	961	18.2
		1	6.3	15018	42.5	667	23.0
		2	7.7	17727	43.6	789	22.6
		3	7.3	16446	47.2	855	19.1
		4	8.9	19827	45.4	862	23.1
	Mean		**7.3**	**17114**	**43.5**	**827**	**21.2**
Standard	**Tower**	**unt**	6.8	12619	54.2	737	17.2
		1	8.0	15161	52.6	858	18.1
		2	7.8	15461	50.5	904	17.1
		3	8.6	15013	57.5	910	16.7
		4	10.0	15509	64.6	872	17.8
	Mean		**8.2**	**14753**	**55.9**	**856**	**17.4**
Standard	**Volume**	**unt**	4.7	11535	42.9	622	19.5
		1	6.8	15333	45.5	625	25.1
		2	7.6	16896	45.4	636	26.9
		3	8.0	16220	51.0	701	23.4
		4	8.7	19655	44.6	595	33.2
	Mean		**7.2**	**15928**	**45.9**	**636**	**25.6**

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	**1**	0.694	ns	0.919	ns	0.399	ns	0.210	ns	0.131	ns
Variety (V)	**1**	0.002	0.4	0.014	1591	<0.001	3.8	0.016	98	0.001	2.9
Fungicide (F)	**4**	<0.001	0.6	<0.001	1728	0.011	4.3	0.703	ns	<0.001	2.5
S&N*V	**1**	0.086	ns	0.153	ns	0.419	ns	0.072	ns	0.245	ns
S&N*F	**4**	0.179	ns	0.290	ns	0.619	ns	0.423	ns	0.779	ns
V*F	**4**	0.781	ns	0.254	ns	0.354	ns	0.164	ns	0.030	4.0
S&N*V*F	**4**	0.092	ns	0.641	ns	0.434	ns	0.408	ns	0.058	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-15. Effects of treatments on the yield and yield components for SRUC 2017. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

SRUC 2017					
S & N rate	**Variety**	**Fungicide**	**Yield t ha^{-1}**	**Grains m^{-2}**	**MGW (mg)**
High	**Tower**	**unt**	6.9	14349	48.4
		1	7.8	15384	50.5
		2	8.3	15235	54.8
		3	8.1	15128	53.8
		4	8.9	15822	56.5
	Mean		**8.0**	**15184**	**52.8**
High	**Volume**	**unt**	7.0	18714	37.3
		1	8.1	21275	38.2
		2	8.5	22816	37.5
		3	9.1	23264	39.4
		4	9.8	24929	39.4
	Mean		**8.5**	**22200**	**38.3**
Standard	**Tower**	**unt**	6.6	14076	47.2
		1	8.0	14635	54.8
		2	7.7	14297	54.1
		3	8.6	15313	56.0
		4	8.7	15854	55.3
	Mean		**7.9**	**14835**	**53.5**
Standard	**Volume**	**unt**	8.1	21252	37.9
		1	8.5	20583	41.4
		2	9.2	22606	40.8
		3	9.1	22679	40.2
		4	9.9	23808	41.7
	Mean		**8.9**	**22186**	**40.4**

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	1	0.211	ns	0.590	ns	0.038	1.2
Variety (V)	1	0.008	0.5	<0.001	1390	<0.001	1.7
Fungicide (F)	4	<0.001	0.3	<0.001	838	<0.001	1.5
S&N*V	1	0.233	ns	0.778	ns	0.364	ns
S&N*F	4	0.464	ns	0.175	ns	0.108	ns
V*F	4	0.279	ns	0.003	1622	0.003	2.4
S&N*V*F	4	0.008	0.7	0.152	ns	0.250	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-16. Effects of treatments on the yield and yield components for Teagasc 2015. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

Teagasc 2015							
S & N rate	**Variety**	**Fungicide**	**Yield t ha^{-1}**	**Grains m^{-2}**	**MGW (mg)**	**Ears m^{-2}**	**Grains ear^{-1}**
High	**Tower**	**unt**	10.4	18663	55.6	970	19.4
		1	11.2	19367	57.8	1016	19.3
		2	11.9	20495	57.8	1066	19.3
		3	11.9	21032	56.8	1090	19.3
		4	12.0	20392	58.9	1059	19.3
	Mean		**11.5**	**19990**	**57.4**	**1040**	**19.3**
High	**Volume**	**unt**	8.2	22116	37.3	612	36.8
		1	10.7	27205	39.3	671	40.6
		2	10.9	27092	40.3	711	38.2
		3	10.8	27049	39.7	699	39.5
		4	10.9	27152	40.3	628	43.6
	Mean		**10.3**	**26123**	**39.4**	**664**	**39.7**
Standard	**Tower**	**unt**	10.4	18318	56.8	888	20.6
		1	10.7	18490	57.9	944	19.7
		2	11.2	18231	61.1	915	20.0
		3	11.5	18955	60.5	900	21.1
		4	11.1	18164	61.2	863	21.3
	Mean		**11.0**	**18432**	**59.5**	**902**	**20.5**
Standard	**Volume**	**unt**	9.8	25645	38.2	608	42.2
		1	10.4	26123	39.7	624	41.8
		2	10.8	26157	41.5	672	39.1
		3	10.9	26318	41.6	660	40.0
		4	10.7	26141	42.3	567	44.0
	Mean		**10.5**	**26077**	**40.6**	**626**	**41.4**

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	1	0.781	ns	0.362	ns	0.339	ns	0.128	ns	0.034	1.3
Variety (V)	1	0.004	0.4	<0.001	617	<0.001	1.0	<0.001	61	<0.001	1.1
Fungicide (F)	4	<0.001	0.3	<0.001	779	<0.001	1.4	0.027	54	0.073	ns
S&N*V	1	0.096	ns	0.024	2265	0.313	ns	0.093	ns	0.634	ns
S&N*F	4	<0.001	1.3	<0.001	2184	0.411	ns	0.448	ns	0.706	ns
V*F	4	0.063	ns	0.036	1107	0.989	ns	0.799	ns	0.153	ns
S&N*V*F	4	0.211	ns	0.079	ns	0.770	ns	0.623	ns	0.478	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-17. Effects of treatments on the yield and yield components for Teagasc 2016. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

			Teagasc 2016				
S & N rate	**Variety**	**Fungicide**	**Yield t ha^{-1}**	**Grains m^{-2}**	**MGW (mg)**	**Ears m^{-2}**	**Grains ear^{-1}**
High	**Tower**	**unt**	7.1	16145	44.2	1093	14.7
		1	8.6	17994	48.0	1126	15.5
		2	9.4	17925	52.4	1031	19.4
		3	9.5	18787	50.5	1061	17.1
		4	9.9	19833	50.1	1090	18.8
	Mean		**8.9**	**18137**	**49.0**	**1080**	**17.1**
High	**Volume**	**unt**	7.3	19424	37.8	623	32.1
		1	8.2	21580	38.2	777	27.6
		2	9.7	24884	38.9	793	31.5
		3	9.7	24272	40.0	809	29.1
		4	10.1	25360	40.0	735	33.5
	Mean		**9.0**	**23104**	**39.0**	**747**	**30.8**
Standard	**Tower**	**unt**	6.7	15045	44.6	1196	12.6
		1	8.5	17236	49.2	901	18.2
		2	9.2	18326	50.3	995	17.9
		3	9.1	17880	51.0	1049	16.9
		4	9.8	18794	52.3	1060	17.0
	Mean		**8.7**	**17456**	**49.5**	**1040**	**16.5**
Standard	**Volume**	**unt**	7.4	19501	38.0	620	31.2
		1	8.8	23336	37.7	551	35.9
		2	9.2	22413	40.8	576	37.0
		3	9.4	24175	38.9	674	34.2
		4	10.3	25716	39.9	648	38.5
	Mean		**9.0**	**23028**	**39.1**	**614**	**35.4**

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	1	0.400	ns	0.477	ns	0.763	ns	0.242	ns	0.297	ns
Variety (V)	1	0.149	ns	<0.001	839	<0.001	1.3	<0.001	85	<0.001	2.5
Fungicide (F)	4	0.431	ns	0.412	ns	0.753	ns	0.224	ns	0.041	2.5
S&N*V	1	<0.001	0.4	<0.001	1404	<0.001	2.5	0.671	ns	0.007	4.8
S&N*F	4	0.441	ns	0.404	ns	0.825	ns	0.071	ns	0.102	ns
V*F	4	0.615	ns	0.032	1215	<0.001	1.9	0.180	ns	0.457	ns
S&N*V*F	4	0.506	ns	0.015	1849	0.092	ns	0.896	ns	0.774	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-18. Effects of treatments on the yield and yield components for Teagasc 2017. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

			Teagasc 2017				
S & N rate	**Variety**	**Fungicide**	**Yield t ha^{-1}**	**Grains m^{-2}**	**MGW (mg)**	**Ears m^{-2}**	**Grains ear^{-1}**
High	**Tower**	**unt**	4.8	10851	44.1	710	17.1
		1	7.5	16849	44.4	976	17.4
		2	7.9	16701	48.9	947	17.3
		3	8.5	16789	50.7	874	19.4
		4	9.4	17693	53.1	905	19.6
	Mean		**7.6**	**15777**	**48.3**	**882**	**18.2**
High	**Volume**	**unt**	6.1	15412	35.3	592	26.6
		1	6.9	19518	36.6	616	32.4
		2	8.5	22057	38.7	662	33.6
		3	8.5	22147	38.8	666	33.4
		4	9.8	24258	40.4	630	38.5
	Mean		**8.0**	**20678**	**38.0**	**633**	**32.9**
Standard	**Tower**	**unt**	4.0	9364	44.0	654	14.7
		1	7.7	16034	47.9	903	17.8
		2	8.0	17029	46.9	835	19.8
		3	9.2	18374	50.1	1056	17.6
		4	9.4	18884	51.0	922	20.6
	Mean		**7.6**	**15937**	**48.0**	**874**	**18.1**
Standard	**Volume**	**unt**	5.2	14467	37.7	448	32.3
		1	7.8	19165	41.0	517	37.3
		2	8.3	21124	39.3	598	35.7
		3	8.4	20959	40.8	486	43.2
		4	9.6	22945	42.0	566	40.8
	Mean		**7.8**	**19732**	**40.2**	**523**	**37.9**

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	1	0.797	ns	0.247	ns	0.194	ns	0.073	ns	0.057	ns
Variety (V)	1	0.130	ns	<0.001	839	<0.001	2.3	<0.001	29	<0.001	1.2
Fungicide (F)	4	<0.001	0.5	<0.001	1229	<0.001	2.0	<0.001	69	<0.001	2.2
S&N*V	1	0.641	ns	0.157	ns	0.231	ns	0.005	65	0.003	2.4
S&N*F	4	0.055	ns	0.806	ns	0.186	ns	0.487	ns	0.788	ns
V*F	4	0.017	0.7	0.325	ns	0.276	ns	0.013	90	0.031	2.9
S&N*V*F	4	0.650	ns	0.506	ns	0.973	ns	0.052	ns	0.051	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-19. Yield relationship with average total disease over the top three leaf layers, and averaged green leaf area (GLA) over the top three leaf layers

Site/season	Growth stage	Average Disease		GLA	
		r^2	p value	r^2	p value
SRUC 2015	31	0.13	<0.001	*	
	59	0.27	<0.001	*	
	69	0.32	<0.001	0.27	<0.001
SRUC 2016	31	0.01	ns	*	
	39	0.07	0.009	*	
	73	0.38	<0.001	0.58	<0.001
SRUC 2017	49	0.08	0.007	*	
	77	0.39	<0.001	0.17	<0.001
Teagasc 2015	31	0.02	ns	*	
	49	0.35	<0.001	*	
	71	0.41	<0.001	0.41	<0.001
Teagasc 2016	31	0.14	<0.001	*	
	49	0.46	<0.001	*	
	75	0.11	0.003	0.5	<0.001
Teagasc 2017	75	0.54	<0.001	0.47	<0.001

Table 2-20. Effects of treatments on screenings (%<2.5mm) and hectolitre weight (HTW) (kg hl^{-1}) for SRUC 2015 Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

SRUC 2015				
S & N rate	**Variety**	**Fungicide**	**Screenings (%<2.5mm)**	**HTW (kg hl^{-1})**
High	**Tower**	**unt**	11.2	59.4
		1	9.8	60.7
		2	8.1	61.0
		3	7.9	61.0
		4	7.3	61.0
	Mean		**8.8**	**60.6**
High	**Volume**	**unt**	36.7	58.8
		1	33.8	59.5
		2	32.1	60.1
		3	29.8	59.6
		4	26.7	59.6
	Mean		**31.8**	**59.5**
Standard	**Tower**	**unt**	11.3	59.9
		1	14.0	59.0
		2	10.6	59.6
		3	10.1	59.7
		4	9.6	60.4
	Mean		**11.1**	**59.7**
Standard	**Volume**	**unt**	32.4	59.1
		1	30.8	59.1
		2	26.7	59.2
		3	30.6	59.2
		4	28.6	60.4
	Mean		**29.8**	**59.4**

Significance	**df**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	**1**	0.908	ns	0.048	0.5
Variety (V)	**1**	<0.001	3.2	0.035	0.6
Fungicide (F)	**4**	<0.001	2.1	0.011	0.6
S&N*V	**1**	0.155	ns	0.176	Ns
S&N*F	**4**	0.221	ns	0.037	0.8
V*F	**4**	0.388	ns	0.982	ns
S&N*V*F	**4**	0.305	ns	0.616	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, HTW = hectolitre weight, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-21. Effects of treatments on screenings (%<2.5mm) and hectolitre weight (HTW) (kg hl^{-1}) for SRUC 2016. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

SRUC 2016				
S & N rate	**Variety**	**Fungicide**	**Screenings (%<2.5mm)**	**HTW (kg hl^{-1})**
High	**Tower**	**unt**	41.2	58.8
		1	41.0	59.0
		2	40.2	59.8
		3	41.1	58.9
		4	41.3	58.8
	Mean		**40.9**	**59.1**
High	**Volume**	**unt**	40.6	59.4
		1	40.8	59.2
		2	42.3	57.7
		3	42.3	57.7
		4	43.5	56.5
	Mean		**41.9**	**58.1**
Standard	**Tower**	**unt**	42.0	58.0
		1	40.6	59.5
		2	40.9	59.2
		3	40.0	60.0
		4	39.4	60.6
	Mean		**40.6**	**59.4**
Standard	**Volume**	**unt**	42.4	57.6
		1	41.5	58.5
		2	41.2	58.8
		3	40.8	59.2
		4	40.2	59.9
	Mean		**41.2**	**58.8**

Significance	**df**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	**1**	0.563	ns	0.563	ns
Variety (V)	**1**	0.109	ns	0.109	ns
Fungicide (F)	**4**	0.932	ns	0.932	ns
S&N*V	**1**	0.725	ns	0.725	ns
S&N*F	**4**	0.071	ns	0.071	ns
V*F	**4**	0.776	ns	0.776	ns
S&N*V*F	**4**	0.750	ns	0.750	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, HTW = hectolitre weight, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-22. Effects of treatments on screenings (%<2.5mm) and hectolitre weight (HTW) (kg hl^{-1}) for SRUC 2017. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

SRUC 2017				
S & N rate	**Variety**	**Fungicide**	**Screenings (%<2.5mm)**	**HTW (kg hl^{-1})**
High	**Tower**	**unt**	11.5	56.8
		1	7.2	58.8
		2	5.4	59.7
		3	5.9	59.0
		4	4.0	60.7
	Mean		**6.8**	**59.0**
High	**Volume**	**unt**	19.5	56.3
		1	16.3	58.4
		2	18.5	57.7
		3	19.3	57.1
		4	14.6	58.4
	Mean		**17.6**	**57.6**
Standard	**Tower**	**unt**	9.8	55.5
		1	4.9	57.0
		2	6.2	57.9
		3	4.1	57.6
		4	3.8	59.0
	Mean		**5.7**	**57.4**
Standard	**Volume**	**unt**	18.1	55.4
		1	14.7	56.6
		2	11.4	57.4
		3	10.9	57.5
		4	10.6	58.6
	Mean		**13.2**	**57.1**

Significance	**df**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	**1**	0.123	ns	0.488	ns
Variety (V)	**1**	<0.001	1.6	0.071	ns
Fungicide (F)	**4**	0.04	2.1	0.208	ns
S&N*V	**1**	<0.001	3.8	<0.001	4.0
S&N*F	**4**	0.473	ns	0.525	ns
V*F	**4**	0.917	ns	0.498	ns
S&N*V*F	**4**	0.171	ns	0.653	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, HTW = hectolitre weight, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-23. Effects of treatments on screenings (%<2.5mm) and hectolitre weight (kg hl^{-1}) for Teagasc 2015. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

Teagasc 2015				
S & N rate	**Variety**	**Fungicide**	**Screenings (%<2.5mm)**	**HTW (kg hl^{-1})**
High	**Tower**	**unt**	1.3	64.2
		1	1.1	65.2
		2	1.1	64.9
		3	0.8	65.4
		4	0.8	65.5
	Mean		**1.0**	**65.0**
High	**Volume**	**unt**	11.3	59.3
		1	6.3	60.4
		2	4.3	61.7
		3	4.4	61.1
		4	4.5	61.6
	Mean		**6.2**	**60.8**
Standard	**Tower**	**unt**	1.7	63.6
		1	0.9	64.7
		2	0.6	65.4
		3	0.8	64.3
		4	0.8	64.7
	Mean		**1.0**	**64.5**
Standard	**Volume**	**unt**	4.9	60.5
		1	6.1	61.6
		2	2.7	62.0
		3	3.9	61.8
		4	2.5	62.6
	Mean		**4.0**	**61.7**

Significance	**df**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	**1**	0.240	ns	0.861	ns
Variety (V)	**1**	0.001	1.7	<0.001	1.2
Fungicide (F)	**4**	0.189	Ns	0.217	ns
S&N*V	**1**	<0.001	2.4	<0.001	2.8
S&N*F	**4**	0.031	2.2	0.905	ns
V*F	**4**	<0.001	1.9	0.528	ns
S&N*V*F	**4**	0.007	2.8	0.498	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, HTW = hectolitre weight, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-24. Effects of treatments on screenings (%<2.5mm) and hectolitre weight (HTW) (kg hl^{-1}) for Teagasc 2016. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

Teagasc 2016				
S & N rate	**Variety**	**Fungicide**	**Screenings (%<2.5mm)**	**HTW (kg hl^{-1})**
High	**Tower**	**unt**	17.2	53.8
		1	8.2	57.1
		2	4.7	57.9
		3	5.7	57.8
		4	6.1	57.9
	Mean		**8.4**	**56.9**
High	**Volume**	**unt**	28.8	52.3
		1	21.1	53.2
		2	17.6	54.6
		3	19.5	55.3
		4	15.3	55.5
	Mean		**20.4**	**54.2**
Standard	**Tower**	**unt**	18.8	53.7
		1	7.8	57.4
		2	6.0	58.3
		3	6.2	58.5
		4	5.2	58.7
	Mean		**8.8**	**57.3**
Standard	**Volume**	**unt**	19.0	52.3
		1	18.4	55.0
		2	14.4	55.9
		3	13.7	56.4
		4	9.3	57.1
	Mean		**14.9**	**55.3**

Significance	**df**	**P**	**LSD**	**P**	**LSD**
S & N rate (S&N)	**1**	0.143	ns	0.275	ns
Variety (V)	**1**	<0.001	0.9	<0.001	0.8
Fungicide (F)	**4**	<0.001	2.9	0.304	ns
S&N*V	**1**	<0.001	3.9	<0.001	1.8
S&N*F	**4**	0.805	ns	0.437	ns
V*F	**4**	0.182	ns	0.129	ns
S&N*V*F	**4**	0.614	ns	0.901	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, HTW = hectolitre weight, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-25. Effects of treatments on screenings (%<2.5mm) and hectolitre weight (HTW) (kg hl^{-1}) for Teagasc 2017. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

Teagasc 2017				
S & N rate	**Variety**	**Fungicide**	**Screenings (%<2.5mm)**	**HTW (kg hl^{-1})**
High	**Tower**	**unt**	13.9	47.5
		1	11.9	53.6
		2	7.3	54.5
		3	5.0	59.8
		4	4.2	60.3
	Mean		**8.5**	**55.1**
High	**Volume**	**unt**	43.2	52.7
		1	32.0	52.8
		2	21.5	57.5
		3	19.4	54.7
		4	12.0	55.2
	Mean		**25.6**	**54.6**
Standard	**Tower**	**unt**	12.9	48.2
		1	8.4	54.5
		2	9.4	53.5
		3	5.6	56.5
		4	5.9	59.9
	Mean		**8.4**	**54.5**
Standard	**Volume**	**unt**	31.4	50.6
		1	19.8	54.3
		2	16.7	55.3
		3	9.7	57.4
		4	10.6	54.1
	Mean		**17.6**	**54.3**

Significance	**df**	**P**	**LSD**	**P**	**LSD**
ns S & N rate (S&N)	**1**	0.010	2.2	0.734	ns
Variety (V)	**1**	<0.001	4.7	0.698	ns
Fungicide (F)	**4**	0.084	3.2	0.847	ns
S&N*V	**1**	<0.001	4.8	<0.001	3.7
S&N*F	**4**	0.080	ns	0.873	ns
V*F	**4**	<0.001	5.7	0.008	3.8
S&N*V*F	**4**	0.753	ns	0.524	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, HTW = hectolitre weight Ns = not significant (p>0.05) The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Field measurements

Lodging & straw breakdown

At no site/season was there a significant variety x fungicide interaction while fungicide programme significantly affected the level of straw breakdown observed at all sites analysed with the exception of Teagasc 2016, with the application of fungicide significantly reducing the level of straw breakdown observed compared to the untreated programme ($p<0.05$) (Table 2-26).

Increasing the S & N rate did not influence the level of straw breakdown observed at any of the five site/season analysed ($p>0.05$). There was significantly more straw breakdown observed in Volume compared to Tower ($p<0.05$) at two site/seasons (SRUC 2017 and Teagasc 2017) while no difference was observed in the other site/seasons ($p>0.05$) (Table 2-26). There were no significant two or three-way interactions ($p>0.05$).

There was minimal lodging observed over the five site/season analysed with significant effects of treatments only observed at Teagasc 2015. At this site, there was only lodging observed at the high S & N rate programme. In Volume the 1 (40%) and 2 (27.5%) spray programmes only which resulted in a significant two-way and three-way interactions between S & N rate x variety, S & N rate x fungicide programme and variety x fungicide programme and S & N rate x variety x fungicide programme while main effects of S & N rate, variety and fungicide were not significant ($p>0.05$) (Table 2-27).

Table 2-26. Effects of treatments on the level of straw breakdown (%) for all site/season. There was no straw breakdown observed at SRUC 2015. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

S & N rate	Variety	Fungicide	SRUC 2016	SRUC 2017	Teagasc 2015	Teagasc 2016	Teagasc 2017
High	**Tower**	**unt**	80.0	62.5	26.2	17.5	52.5
		1	76.2	22.5	7.8	12.5	32.5
		2	41.2	2.5	4.0	10.0	20.0
		3	33.8	8.0	2.7	20.0	18.8
		4	3.8	0.0	4.0	3.8	2.5
	Mean		**47.0**	**19.1**	**8.9**	**12.8**	**25.3**
High	**Volume**	**unt**	80.0	41.2	22.5	46.2	98.8
		1	57.5	38.8	8.8	1.2	75.0
		2	16.7	27.5	16.2	1.2	47.5
		3	37.5	16.3	13.8	0.0	37.5
		4	15.7	6.3	7.5	15.0	10.0
	Mean		**41.5**	**26.0**	**13.8**	**12.7**	**53.8**
Standard	**Tower**	**unt**	90.0	28.8	14.5	8.8	52.5
		1	66.2	3.8	7.7	2.5	41.2
		2	60.0	0.0	1.2	25.0	17.5
		3	56.3	0.0	1.0	31.2	20.0
		4	2.7	0.0	2.2	47.5	5.0
	Mean		**55.0**	**6.5**	**5.3**	**23.0**	**27.2**
Standard	**Volume**	**unt**	71.2	67.5	27.5	27.5	92.5
		1	76.2	45.0	18.7	31.2	62.5
		2	31.2	20.0	18.0	28.8	58.8
		3	15.0	13.5	17.5	12.5	50.0
		4	8.8	5.0	10.5	7.5	22.5
	Mean		**40.5**	**30.2**	**18.4**	**21.5**	**57.3**

Significance	df	P	LSD	P	LSD	P	LSD	P	LSD	P	LSD
S & N rate (S&N)	**1**	0.472	ns	0.359	ns	0.900	ns	0.569	ns	0.868	ns
Variety (V)	**1**	0.096	ns	0.012	10.5	0.087	ns	0.917	ns	0.008	18.2
Fungicide (F)	**4**	<0.001	13.5	<0.001	10.5	0.002	8.3	0.561	ns	<0.001	12.0
S&N*V	**1**	0.408	ns	0.099	ns	0.38	ns	0.917	ns	0.923	ns
S&N*F	**4**	0.603	ns	0.986	ns	0.896	ns	0.205	ns	0.848	ns
V*F	**4**	0.101	ns	0.150	ns	0.617	ns	0.055	ns	0.134	ns
S&N*V*F	**4**	0.115	ns	0.019	ns	0.936	ns	0.075	ns	0.542	ns

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Table 2-27. Effects of treatments on the level of lodging (%) observed for all site/season. There was no lodging observed at SRUC 2015. Means, p and LSD values presented were produced by split-split plot ANOVA analysis.

S & N rate	Variety	Fungicide	SRUC 2016	SRUC 2017	Teagasc 2015	Teagasc 2016	Teagasc 2017
High	**Tower**	**unt**	8.8	0.0	0.0	0.0	0.0
		1	0.0	0.0	0.0	1.2	0.0
		2	0.0	0.0	0.0	7.5	0.0
		3	0.0	0.0	0.0	0.0	0.0
		4	0.0	0.0	0.0	18.8	0.0
	Mean		**1.8**	**0.0**	**0.0**	**5.5**	**0.0**
High	**Volume**	**unt**	11.2	0.0	40.0	22.5	0.0
		1	5.0	5.0	27.5	21.2	0.0
		2	2.5	10.0	0.0	20.0	0.0
		3	6.2	12.5	0.0	12.5	0.0
		4	11.2	0.0	0.0	10.0	5.0
	Mean		**7.2**	**5.5**	**13.5**	**17.2**	**1.0**
Standard	**Tower**	**unt**	0.0	0.0	0.0	0.0	0.0
		1	0.0	0.0	0.0	12.5	0.0
		2	0.0	0.0	0.0	1.2	0.0
		3	0.0	0.0	0.0	0.0	0.0
		4	0.0	0.0	0.0	0.0	0.0
	Mean		**0.0**	**0.0**	**0.0**	**2.7**	**0.0**
Standard	**Volume**	**unt**	21.2	0.0	0.0	0.0	0.0
		1	0.0	0.0	0.0	0.0	0.0
		2	0.0	3.8	0.0	5.0	0.0
		3	0.0	0.0	0.0	2.5	0.0
		4	0.0	0.0	0.0	0.0	0.0
	Mean		**4.2**	**0.8**	**0.0**	**1.5**	**0.0**

Significance	df	P	LSD	P	LSD	P	LSD	P	LSD	P	LSD
S & N rate (S&N)	**1**	0.596	ns	0.472	ns	0.113	ns	0.430	ns	0.391	1.6
Variety (V)	**1**	0.204	ns	0.303	ns	0.068	ns	0.245	ns	0.356	1.2
Fungicide (F)	**4**	0.861	ns	0.425	ns	0.068	ns	0.162	ns	0.356	1.6
S&N*V	**1**	0.125	ns	0.307	ns	0.042	9.9	0.878	ns	0.417	1.6
S&N*F	**4**	0.958	ns	0.556	ns	0.042	12.3	0.881	ns	0.417	2.3
V*F	**4**	0.712	ns	0.307	ns	0.042	12.1	0.651	ns	0.417	2.2
S&N*V*F	**4**	0.413	ns	0.556	ns	0.042	17.1	0.396	ns	0.417	3.2

Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray, Ns = not significant (p>0.05). The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

2.3.2 Investigating the response to late-season disease control in six and two-row varieties

Meteorological data

The growing season for both sites is defined as the period between October and July. Data for the KIL is not available. The 2018 growing season was warmer and drier than average with a seasonal mean temperature of 9.3°C (long term (1981-2010) average = 8.9°) and total rainfall of 591mm (long term average rainfall = 699 mm) for the growing season. It must be noted that May and June were extremely warm with little or no rainfall occurring (Figure 2-4), this lead to drought conditions with soil moisture deficits in excess of 80mm. Cumulative global radiation at the OP site was higher than average at 2974 MJ m^{-2} (seasonal average (2008-2014) = 2698 MJ m^{-2}).

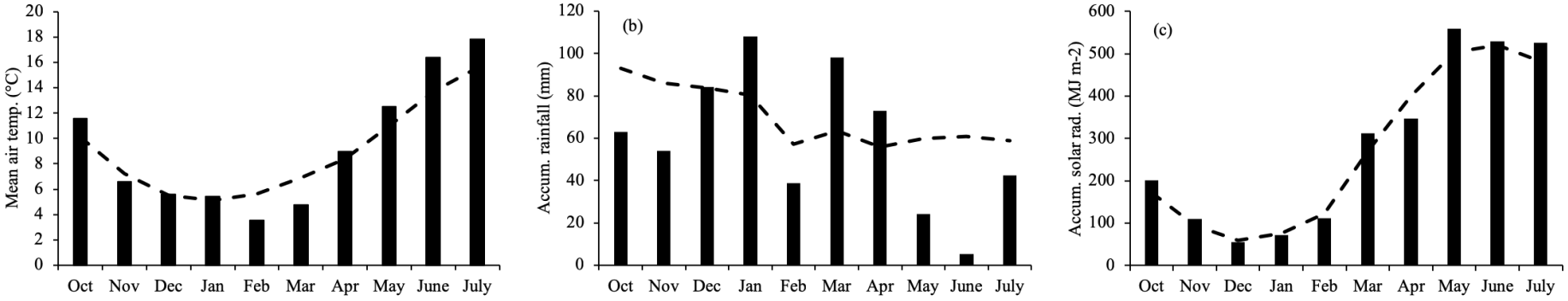

Figure 2-4. Meteorological data from October to July for the OP site (a) Monthly accumulated rainfall (mm),(b) Monthly mean temperature (°C) and Monthly accumulated global radiation (MJ m^{-2}). Broken line shows long term averages (for (a) and (b) period 1981-2010) and for (c) period 2008-2014)

Disease

A disease assessment at GS49 was carried out on Leaf 3 (L3) and leaf 4 (L4) at the Oak Park site, while no assessment was carried out at this stage at KIL due to no disease being present on the top 4 leaves. The level of disease was very low (Average disease L3 & L4 = 1.2%) for the Oak Park (OP) assessment indicating that the cover sprays at GS25 and GS31/32 controlled disease effectively, while no difference in the level of disease was observed between the varieties ($p<0.05$).

The diseases that were present at the GS75 assessment at both sites varied between varieties, although in all varieties the level of infection was dominated by ramularia. In addition to ramularia, both Volume and Tower had low levels of Septoria nodorum infection while low levels of the spot form of net blotch were present in Kosmos and rhynchosporium was present in Cassia.

At both sites, the variety x fungicide interaction was not significant ($p>0.05$), but there was a significant effect of fungicide treatment on the level of disease observed ($p<0.05$). The 2 spray programme had the highest level of disease with a significant reduction in disease observed in the 3 spray programme ($p<0.05$). The response to the remaining programme varied between the sites, at the KIL site there was a further significant decrease in the level of disease observed for all treatments containing CTL while there was no difference observed between these treatments (Table 2-28). For the Oak Park site again there was a further decrease from treatment containing CTL although delaying CTL application to GS65 had significantly higher disease levels compared to treatments where CTL was applied at GS49 ($p<0.05$). There was a significant effect of variety on the level of disease observed at both sites ($p<0.05$) (Table 2-28). At the KIL site, Kosmos had the highest level of infection (average L1 & L2 = 9.3%) while no difference was observed between the other varieties ($p>0.05$). At Oak Park, Tower and Volume have significantly more disease compared to Cassia and Kosmos ($p<0.05$).

Green leaf area

The variety x fungicide interaction was not significant ($p>0.05$) at either site, while Fungicide treatment significantly affected GLA ($p<0.05$), The 2 spray programme had the

lowest GLA level of all treatments, followed by the 3 spray programme at both sites. At the OP site, all treatments containing CTL significantly increased the GLA compared to the 2 and 3 spray programmes ($p<0.05$), while there was no difference between these treatments ($p>0.05$). At the KIL site there was a similar increase from treatments containing CTL although applying CTL at GS49 and GS65 increased GLA significantly compared to just one application at GS65 (4 spray programme) ($p<0.05$), while there was no difference between the 4 spray, 3 spray + CTL and 4 spray + proline ($p>0.05$).

There was no significant effect of variety on the GLA at the KIL site ($p>0.05$) while the effect was significant at OP ($p<0.05$) (Table 2-28). Kosmos had the highest GLA, followed by Cassia while Tower and Volume have the lowest GLA.

Table 2-28. The effects of treatments on average disease and GLA for the top three leaf layers for Kildalton (KIL) and Oak Park (OP). P Values and means (back-transformed) were produced from a split-split plot ANOVA analysis.

		Avg Dis L1 & L2		Avg GLA L1 & L2	
Variety	**Fungicide**	**OP**	**KIL**	**OP**	**KIL**
Cassia	**2 spray**	27.7	33.9	28.9	11.4
Cassia	**3 spray**	14.5	31.1	57.3	13.6
Cassia	**4 spray**	2.0	0.7	84.3	52.4
Cassia	**3 spray + CTL**	1.1	0.6	85.1	48.8
Cassia	**4 spray + CTL**	1.0	0.3	84.5	55.6
Cassia	**4 spray + proline**	1.0	0.4	87.7	49.0
	mean	7.9	11.2	71.3	38.5
Kosmos	**2 spray**	13.9	44.7	67.0	15.9
Kosmos	**3 spray**	17.1	36.0	63.1	22.3
Kosmos	**4 spray**	4.7	1.0	87.5	67.9
Kosmos	**3 spray + CTL**	1.5	1.7	94.8	62.9
Kosmos	**4 spray + CTL**	1.6	1.5	94.8	68.5
Kosmos	**4 spray + proline**	1.4	1.6	93.7	70.8
	mean	6.7	14.4	83.5	51.4
Tower	**2 spray**	37.4	35.0	14.7	8.1
Tower	**3 spray**	18.2	22.7	40.5	19.1
Tower	**4 spray**	8.9	0.7	65.6	62.1
Tower	**3 spray + CTL**	1.6	0.5	77.7	67.6
Tower	**4 spray + CTL**	1.5	0.5	85.3	60.4
Tower	**4 spray + proline**	1.4	1.8	80.5	59.5
	mean	11.5	10.2	60.7	46.1
Volume	**2 spray**	37.4	41.6	17.5	9.9
Volume	**3 spray**	20.8	16.3	43.3	24.3
Volume	**4 spray**	3.8	1.1	83.3	57.7
Volume	**3 spray + CTL**	2.6	1.0	86.8	57.9
Volume	**4 spray + CTL**	1.9	0.3	89.9	54.9
Volume	**4 spray + proline**	1.6	0.6	81.0	62.7
	mean	11.3	10.2	67.0	44.6
Significance	**df**	P	P	P	P
Variety (V)	**3**	0.012	0.024	0.001	0.092
Fungicide (F)	**5**	<.001	<.001	<.001	<.001
V x F	**15**	0.139	0.067	0.191	0.856

[1] Average area infected by disease for leaf 1 and leaf 2. [2] Average green leaf area for leaf 1 and leaf 2. Ns = not significant (p>0.05). The residual d.f were 9 and 60 for the main plot and sub-plot respectively.

Yield

The variety x fungicide interaction was not significant ($p>0.05$), while fungicide treatment significantly influenced yield ($p<0.05$). This effect was caused by the 2 & 3 spray programmes producing the lowest yield ($p<0.05$), there was no significant benefit on yield from the application of the 4 spray + proline programme ($p>0.05$), while the 4 spray, 3 spray + CTL, and 4 spray + CTL all provided a significant yield increases compared to the 2 and 3 spray programmes ($p<0.05$), with no statistical difference being observed between those programmes ($p>0.05$). There was no difference in the yield produced by the four varieties ($p>0.05$).

Yield components

For both grains, m^{-2} and MGW the variety x fungicide interaction was not significant ($p>0.05$), while the main effect of fungicide was also not significant for either yield components ($p<0.05$)

There was a significant difference in the grains m^{-2} produced between the four varieties ($p<0.05$). Volume had the highest grains m^{-2} with a significant reduction on this value in Kosmos ($p<0.05$), while the two-rowed varieties produced the lowest but did not differ between each other ($p>0.05$).

There was a significant difference in the MGW produced by the four varieties ($p<0.05$). Tower had the highest MGW, significantly higher than both the six-row varieties ($p<0.05$) but not Cassia ($p>0.05$). There was no difference between Cassia and Kosmos, although both had a significantly larger MGW compared to Volume ($p<0.05$).

Grain quality

There was a significant variety effect on HTW at both sites. Cassia had the highest HTW at both sites while Volume had the lowest HTW ($p<0.05$). There was no difference in HTW between Kosmos and Tower at either site ($p>0.05$).

For both sites, there was a significant fungicide effect on HTW ($p<0.05$), while a significant variety x fungicide interaction occurred at KIL ($p<0.05$) caused by fungicide treatment not affecting HTW in cassia. The general trend was that treatments containing CTL had the highest HTW (Table 2-30).

Volume had the highest level of screenings at both sites ($p<0.05$) while there was no difference observed between Cassia, Tower and Kosmos ($p>0.05$). Like HTW at both sites there was a significant effect of fungicide on the level of screenings recorded at both sites ($p<0.05$), while at OP, there was a significant variety x fungicide interaction ($p<0.05$) due to the magnitude of the response in the different varieties. The trend was that fungicide treatment decreased the level of screenings (Table 2-30).

Table 2-29. The effects of treatments on yield and yield components at Oak Park (OP). P Values, LSD's and means were produced from a split-split plot ANOVA analysis.

Variety	Fungicide	Yield t ha^{-1}	Grains m^{-2}	MGW (mg)
Cassia	**2 spray**	8.17	19024	43.74
	3 spray	8.60	19204	44.86
	4 spray	8.71	19961	44.12
	3 spray + CTL	9.16	19446	47.23
	4 spray + CTL	9.01	20442	45.6
	4 spray + proline	8.78	18760	46.76
	Mean	**8.74**	**19473**	**45.39**
Kosmos	**2 spray**	8.78	23057	38.19
	3 spray	8.84	21562	41.39
	4 spray	9.23	21481	43.09
	3 spray + CTL	9.07	22830	39.81
	4 spray + CTL	9.80	22285	44.35
	4 spray + proline	9.09	22767	39.92
	Mean	**9.14**	**22330**	**41.13**
Tower	**2 spray**	8.10	17449	46.77
	3 spray	7.90	17787	44.49
	4 spray	9.47	21441	45.2
	3 spray + CTL	9.13	19191	47.66
	4 spray + CTL	9.14	18481	49.48
	4 spray + proline	8.71	20303	43.64
	Mean	**8.74**	**19109**	**46.21**
Volume	**2 spray**	8.53	27543	30.98
	3 spray	8.41	25587	33.05
	4 spray	8.99	25580	35.12
	3 spray + CTL	9.78	26641	36.54
	4 spray + CTL	9.81	27560	35.61
	4 spray + proline	8.75	24875	34.93
	Mean	**9.05**	**26298**	**34.37**

Significance	d.	P	LSD	P	LSD	P	LSD
Variety (V)	**3**	0.557	ns	<0.001	2181	<0.001	4.43
Fungicide (F)	**5**	<0.001	0.51	0.865	ns	0.055	ns
V x F	**15**	0.787	ns	0.827	ns	0.589	ns

Ns = not significant (p>0.05), MGW = mean grain weight. The residual d.f were 9 and 60 for the main plot and sub-plot respectively.

Table 2-30. The effects of treatments on screenings (%<2.5mm) and hectolitre weight (kg hl^{-1}) at Kildalton (KIL) and Oak Park (OP). P Values, LSD's and means were produced from a split-split plot ANOVA analysis.

		OP		KIL	
Variety	**Fungicide**	**HTW (kg hl^{-1})**	**Screenings (%<2.5mm)**	**HTW (kg hl^{-1})**	**Screenings (%<2.5mm)**
Cassia	**2 spray**	62.9	10.1	65.3	8.8
	3 spray	63.9	7.4	64.8	8.4
	4 spray	64.6	7.6	64.9	5.1
	3 spray + CTL	66.2	5.2	64.3	6.4
	4 spray + CTL	62.9	10.3	65.2	5.2
	4 spray + proline	65.2	5.4	65.2	5.3
	mean	**64.3**	**7.7**	**64.9**	**6.5**
Kosmos	**2 spray**	59.1	9.8	60.6	10.7
	3 spray	60.4	8.6	62.0	8.9
	4 spray	61.3	5.6	64.6	4.9
	3 spray + CTL	59.9	6.8	64.1	5.4
	4 spray + CTL	62.3	4.8	62.4	5.3
	4 spray + proline	60.6	9.4	63.3	4.4
	mean	**60.6**	**7.5**	**62.8**	**6.6**
Tower	**2 spray**	60.0	11.0	59.3	9.0
	3 spray	60.4	10.2	62.2	6.6
	4 spray	63.3	6.2	64.3	5.5
	3 spray + CTL	62.2	7.4	64.3	5.2
	4 spray + CTL	63.6	6.5	63.5	5.1
	4 spray + proline	62.0	8.1	63.8	4.9
	mean	**61.9**	**8.2**	**62.9**	**6.0**
Volume	**2 spray**	57.2	31.0	56.9	28.2
	3 spray	58.4	27.0	55.9	23.0
	4 spray	59.7	19.5	60.5	18.4
	3 spray + CTL	60.8	14.6	60.9	18.7
	4 spray + CTL	62.0	15.3	60.0	18.5
	4 spray + proline	59.4	18.9	59.8	18.8
	mean	**59.6**	**21.0**	**59.0**	**20.9**

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**3**	0.004	2.1	<0.001	4.6	0.003	2.5	<0.001	2.3
Fungicide (F)	**5**	<0.001	1.2	<0.001	2.7	<0.001	1.1	<0.001	1.5
V x F	**15**	0.146	ns	0.007	6.5	0.027	3.1	0.152	ns

[1]HTW = hectolitre weight, Ns = not significant (p>0.05). The residual d.f were 9 and 60 for the main plot and sub-plot respectively.

Straw breakdown

There was a significant variety x fungicide interaction at the KIL site ($p<0.05$). Fungicide treatment did not influence the level of breakdown in the two-rowed varieties (Cassia and Tower) or Volume, while there were significant fungicide effects in Kosmos. The effect observed in Kosmos was that the 2 spray and 3 spray programmes (programmes without CTL) had the highest level of straw breakdown while treatments including CTL had significantly lower levels of straw breakdown ($p<0.05$) (Table 2-31). Fungicide treatment had no significant influence on the level of straw breakdown observed at Oak Park in any variety ($p<0.05$).

Variety had a significant effect on the level of straw breakdown, which occurred at each site ($p<0.05$). At OP Volume had significantly more straw breakdown compared to the rest of the varieties, while there was no difference between the Tower, Cassia and Kosmos. At KIL, Volume again had the highest level of straw breakdown followed by Kosmos, while Tower and Cassia had the lowest levels.

Table 2-31. The effects of treatments on the level of straw breakdown (%) at Kildalton (KIL) and Oak Park (OP). P Values, LSD's and means were produced from a split-split plot ANOVA analysis.

		% Straw breakdown	
Variety	**Fungicide**	**OP**	**KIL**
Cassia	**2 spray**	1.2	3.8
	3 spray	0.0	2.8
	4 spray	0.0	0.8
	3 spray + CTL	0.0	1.0
	4 spray + CTL	1.2	0.5
	4 spray + proline	0.0	0.5
	Mean	**0.4**	**1.6**
Kosmos	**2 spray**	3.0	50.0
	3 spray	1.2	50.0
	4 spray	1.2	12.8
	3 spray + CTL	3.7	20.8
	4 spray + CTL	5.0	4.0
	4 spray + proline	0.0	16.8
	Mean	**2.4**	**25.7**
Tower	**2 spray**	3.0	0.0
	3 spray	1.3	0.0
	4 spray	0.0	0.0
	3 spray + CTL	0.0	0.0
	4 spray + CTL	0.0	0.0
	4 spray + proline	0.0	0.0
	Mean	**0.7**	**0.0**
Volume	**2 spray**	47.5	72.5
	3 spray	45.0	75.0
	4 spray	38.8	75.0
	3 spray + CTL	42.5	67.5
	4 spray + CTL	48.8	87.5
	4 spray + proline	25.0	80.0
	Mean	**41.3**	**76.3**

Significance	**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**3**	<0.001	12.9	<0.001	15.9
Fungicide (F)	**5**	0.333	ns	0.246	ns
V x F	**15**	0.842	ns	0.044	ns

Ns = not significant (p>0.05). The residual d.f were 9 and 60 for the main plot and sub-plot respectively.

2.4 Discussion.

The results of these studies show that the yield components of a two- and six-row barley differ, with a six-row variety producing a lower number of ears m^{-2} and higher number of grains ear^{-1} cumulating in a higher number of grains m^{-2}, while producing a lower average grain weight compared to a two-row variety, in agreement with previous studies (Garcia del Moral et al., 2003, Arisnabarreta and Miralles, 2015). This study did not find that hybrid varieties produce higher yield compared to conventional varieties contrary to findings of other studies (Longin et al., 2012, Mühleisen et al., 2013). In the six comparisons only one site/season combination (SRUC 2017) did the hybrid six-row (Volume) produce a higher yield compared to the conventional two-row (Tower) across both S & N rates and fungicide programmes, while in the second experiment the hybrid six-row variety produced a similar yield to two conventional two-rowed varieties and a conventional six-row variety.

It is claimed that hybrid six-row varieties have superior disease resistance compared to conventional varieties, although evidence of this has not been published. Disease ratings between Tower and Volume are similar, with the only differences being the genetic resistance to rhynchosporium (6 in Tower and 7 in Volume), net blotch (5 in Tower and 7 in Volume) (Anon., 2017) and brown rust (6 in Tower and 5 in Volume) (AHDB, 2018). This, in part, explains significant differences in average disease levels. At SRUC 2015, the main disease present was rhynchosporium, explaining why Tower had higher levels of disease compared to Volume. At SRUC 2016 early season disease was dominated by mildew and rhynchosporium, thus it is not surprising that Tower had higher levels compared to Volume mainly caused by higher levels of rhynchosporium in Tower (data not presented). At the same site season, brown rust developed late-season explaining why Volume then had higher average levels of disease compared to Tower. Higher levels of disease in Volume compared to Tower at SRUC 2017 could not be explained by differences in ratings, as the main diseases present were mildew and net blotch, although there was no significant difference in the level of net blotch in both varieties, mildew was significantly higher in Volume compared to Tower. This higher level of mildew in Volume compared to Tower was also the cause of the significant difference between varieties at Teagasc 2015 GS69. In the second, the main disease present was ramularia. However, the department of agriculture, food and Marine (DAFM) do not publish resistance to ramularia on the national recommended list.

There was no benefit of using higher seed and nitrogen rates, 25% above the standard, to yield or yield components. Although, the experiment was not designed to test seed and N rate response in both varieties, rather both the inputs were used as a tool to increase grains m-2 in order to test if response to fungicide changed. Therefore it is not surprising that a response was not seen as the sensitivity at the main plot level was low. Additionally the studies have shown that increasing both inputs by greater that 25% had no effect on yield. Increasing seed rate by 100% (200-400 seed m^{-2}) had no effect on yield in spring-sown barley (O'Donovan et al., 2011), while increasing N from 0 kg N ha^{-1} to 120 kg N ha^{-1}, did increase yield, although there was no S x N rate interaction indicating the response to N treatment was the same at both seed rates. The N rate used by O'Donovan et al. (2011) is much lower than used in the current study. Hackett (2016) presented results showing no yield benefit in a hybrid six-row and conventional two and six-row winter barley variety from increasing N rate from 180 to 220 kg N ha^{-1}. Although, the seed suppliers advise that hybrid varieties should be shown at a lower seed rate compared to conventional varieties to avail of the early vigour and potentially offset the higher seed cost (Anon., 2019). The results of this present study support this recommendation as increasing the seed rate to that of a standard rate for a conventional variety showed no benefit in yield.

The yield response to fungicide treatment varied with site and season. When looking at the individual timings, the most significant response was to the GS31/32 timing followed by the GS49 timing, which is an agreement with previous studies carried out in similar environments on winter and spring barley (Walters et al., 2012, Glynn and Grace, 2017, Bingham et al., 2012). The GS31/32 timing significantly reduced disease in low and high pressure seasons, while the additive effect of the GS49 timing only reduced disease significantly when disease pressure was high.

The main hypothesis of this experiment was that a six-row variety would have a greater requirement for late-season disease control compared to a two-row variety. In the first experiment across six site/season combinations, both S & N rate treatments, both varieties responded similarly to the 4 spray programme in both foliar disease control and yield. Disease levels in the untreated programme caused the one site where there was a significant variety x fungicide interaction. While in the second experiment, both conventional two-row, conventional and hybrid six-row varieties again responded similarly to fungicide treatment. On this basis, there is no requirement to alter fungicide timing based on row type.

However, the significant yield increase to the GS65 timing at five out of six site/seasons in both varieties is a result which was not seen previously in an experiment carried out across eight site/seasons from the period of 2010 to 2013 (Glynn and Grace, 2017). When late-season disease pressure was high, there was a significant benefit from the addition of the GS65 timing on foliar disease control. This benefit of late-season disease control could have been due to the inclusion of chlorothalonil (CTL) in the GS65 timing. As mentioned in recent times decreased sensitivity of ramularia has developed to QoI's (Matusinsky et al., 2010), azole's (Piotrowska et al., 2016) and SHDI's (Piotrowska et al., 2017), leaving CTL as the main method of chemical control. Current advice is to include CTL at GS49 for effective ramularia control (Havis et al., 2015), this was not done in this experiment as at the time of design the major fungicide groups were providing effective control. Although, when CTL was included at GS49, as was in the second experiment, disease was effectively controlled. This control of disease led to there being no benefit of the GS65 timing either row-types.

Additionally, at some sites where there was a significant yield response to the GS65 timing, it was caused by an increase in grains m^{-2}. This GS65 application is beyond the period of grain number determination for both row types (Arisnabarreta and Miralles, 2008a, Alqudah and Schnurbusch, 2014), thus the increase in grain number could have been due to a control of FHB, as FHB infection has been shown to reduce grains m^{-2} (Cosic et al., 2007). When assessed, there was a significant reduction in FHB infection from the application of the GS65 timing compared to the other programmes. Although the effect of the GS65 timing on FHB control could not be tested in the second experiment as the 2018 season was extremely dry and warm during anthesis, conditions not suitable for FHB infection, thus no infection occurred.

It was hypothesised that the differences in source-sink balance between two and six-row varieties would lead to differences in response to fungicide, with a six-row variety being more source-limited that a two-row. Response to fungicide was similar in both varieties, although the response to late-season fungicide application could be down to a change in the current understanding of the source-sink balance in winter barley. Previously two-row winter barley has been shown to be sink-limited in an experiment carried out in 2001-2003 (Bingham et al., 2007a). The maximum yield achieved in the study conducted by Bingham et al., (2007a) was 9.4 t ha^{-1} at 100% dry matter (10.8 t ha^{-1} at 85% dry matter), while the maximum yield in this study was 12.8 t ha^{-1}, thus it is possible that in the period between

studies that yield potential of modern varieties could have increased. This increase in yield potential could have altered the source-sink balance, increasing sink size, in turn, increasing the demand for assimilate during grain filling. If true, it would be expected that MGW would be increased from late-season application of fungicide, however, in the present study, MGW was not significantly increased when comparing the 3 and 4 spray programmes with the yield increase from the 4 spray programme mainly coming from an increase in grains m^{-2}.

2.5 Conclusion

The main findings of this study are that across a range of seasons, disease pressures and S & N rate programmes that the yield and response to fungicide did not differ between a hybrid six-row variety and a conventional two-row variety, thus there is no requirement to alter disease management strategy based on row type. The response to late-season disease control in both varieties in the first experiment could be attributed to the failure to effectively control ramularia at GS49.

Chapter 3 **Investigating the source-sink balance in a hybrid six-row and conventional two-row winter barley variety where disease is controlled and uncontrolled.**

3.1 Introduction

Yield formation can be analysed in terms of sink or source limitation of grain filling. ‘Sink-limitation’ refers to a limitation imposed by the number of grains the crop can set and their capacity for storing starch (potential grain weight; PGW). ‘Source-limitation', on the other hand, refers to situations where the supply of assimilates for grain filling is insufficient to meet PGW (Borrás et al., 2004). The sink capacity is determined by developmental events occurring before and shortly after anthesis. The critical period for grain number determination in barley is from the onset of stem extension until awn emergence (Arisnabarreta and Miralles, 2008a, Alqudah and Schnurbusch, 2014), while there is evidence in the literature that PGW can be affected by both pre and post-anthesis development. Thus positive associations have been reported between carpel weight, established before anthesis, and final grain weight of wheat and barley (Calderini et al., 1999, Xie et al., 2015) and also the number of endosperm cells produced during early grain development and grain weight in barley (Cochrane and Duffus, 1983).

The source capacity of a crop is influenced by its ability to intercept light, the efficiency that this energy is converted into biomass and the amount of stored reserves remobilised during grain filling. A number of experiments have been reported in which assimilate supply was manipulated during grain filling, and the response in grain weight did not match the relative change in predicted assimilate supply (Borrás et al., 2004). This has given rise to the concept that grain filling can be ‘co-limited’ by both source and sink, although the metabolic and cellular basis of co-limitation has not been elucidated.

Whether yield of a crop is source-, sink- or co-limited has significant practical implications for disease management. The current understanding is that yield is sink-limited in two-row winter barley (Bingham et al., 2007a), which has led to the formation of a disease management strategy that focusses on protecting the canopy during the period of sink formation (Glynn and Grace, 2017). Conversely winter wheat has been shown to have a

degree of co-limitation (Lynch et al., 2017a, Beed et al., 2007, Collin et al., 2018), which has led to a disease management strategy where maintenance of green area during grain filling is the main focus (Lynch et al., 2017c).

Among the published literature the most popular method for testing the relative source-sink balance during grain filling has been to deliberately manipulate the assimilate supply per unit grain number during grain filling and measure the change in grain weight that results. Sink-limited crops are expected to be less responsive to treatments that either decrease or increase the assimilate supply per grain than source-limited crops. Shading the crop canopy, thus reducing the amount of light the crop can intercept has been used to reduce source capacity relative to sink in barley (Serrago et al., 2013), wheat (Caldiz and Sarandón, 1988, Fischer and HilleRisLambers, 1978, Savin and Slafer, 1991, Grabau et al., 1990) and soyabean (Andrade and Ferreiro, 1996, Egli and Bruening, 2001). Partial de-graining has been used to increase source capacity relative to sink during grain filling in barley (Voltas et al., 1997, Serrago et al., 2013) and wheat (Calderini and Reynolds, 2000). An alternative method for assessing the source-sink balance is to estimate the potential assimilate supply per grain during grain filling from measurements of light interception by the crop, the radiation use efficiency (RUE) and the amount of water-soluble carbohydrates (WSC) at anthesis and to compare this estimate to the achieved grain weight as described by (Bingham et al., 2007a). The method described allows for a more quantitative interpretation of the source-sink balance during grain filling compared to the manipulation of assimilate supply. The latter can describe if a crop is source, sink or co-limited, but the strength of the limitation is difficult to interpret.

Most of the above-mentioned investigations of the source-sink balance have been carried out on healthy crops. As discussed previously, cool temperate climates provide the ideal conditions for the development of fungal pathogens (Zhan et al., 2008). The effects of pathogens on crop growth are documented in section 1.6.2. The effect of disease on yield depends to a large extent on what stage of crop development the epidemic occurs. For example, early-season infections during the stem extension period coincide with the period of spikelet production and tiller survival and thus have the potential to reduce the number of ears m^{-2} and grains ear^{-1} (Lim and Gaunt, 1986, Arisnabarreta and Miralles, 2008a, Kennedy et al., 2016). Late-season disease that develops after the sink capacity is set reduces yield by reducing the availability of assimilate for grain filling. Serrago and Miralles, (2014)

presented evidence of the impact of leaf rust on the source-sink balance in a wheat crop. They concluded that late-season leaf rust infection altered the balance from that of sink limitation in a healthy crop to that of source limitation in an infected crop as the crops ability to provide assimilate during grain filling was reduced. It is accepted that two-row barley is generally more sink-limited than wheat (Serrago et al., 2013), thus barley may be more tolerant of late-season disease than wheat as there appears to a surplus of assimilate supply for grain filling (Bingham et al., 2009; Bingham et al., 2019).

At present, there is little information on the relative source-sink balance of the different ear types of barley. Results of the previous chapter show that, surprisingly, the response of cv Tower and cv Volume to fungicide timing and disease control were similar in spite of the much larger number of grains produced by the six-row variety. This would suggest that the source-sink balance of the two varieties was comparable. Therefore the objective of experiments reported here was to quantify the relative source-sink balance of cv Tower and cv Volume grown with and without fungicide treatment to control disease. The specific hypotheses tested were:

1) In spite of differences in the number of grains produced m^{-2} the source-sink balance of a hybrid six-row variety (Volume) is comparable to that of a conventional two-row variety (Tower).
2) Two- and six-row barley crops that are not treated with fungicide will be more source-limited during grain filling than crops that are treated.

3.2 Materials and methods

3.2.1 Site details and general husbandry

Field experiments were conducted in 2015/16 (hereafter called 2016) and 2016/17 (2017) growing seasons at Teagasc, Oak Park, Carlow, Ireland. The soil type was a loam with moderate moisture-holding capacity. In each season the previous crop was winter wheat. Plots 2.5 x 12m were established following inversion ploughing and harrowing. Seed treated with Redigo Deter ® (50 g l^{-1} prothioconazole and 250 g l^{-1} clothianidin, Bayer Crop Science, Monhem am Rhein, Germany) was drilled on the 30th September 2015 and 30th October 2016 with a Wintersteiger Plotseed XL drill (Wintersteiger AG, Austria). The seed and nitrogen (N) rates used are listed in (Table 3-1). The N fertiliser was applied in two applications, 33% of the total at mid to late tillering (growth stage (GS) 25-29) (Zadoks et al., 1974) and 66% of the total at the onset of stem extension (GS30/31). Other nutrients (P, K and S) were applied at rates to avoid limitations to crop growth and development, in accordance with the regulations governing Ireland (Wall and Plunkett, 2016). Herbicides were applied to ensure weeds did not compete with the crop. To prevent lodging plots received plant growth regulator (PGR) treatment at GS30 and GS37 as presented in appendix 2.

Table 3-1. Seed rate (seeds m^{-2}) and nitrogen (N) (kg N ha^{-1}) programmes

Variety Type	Variety	Seed rate	N rate
		Seeds m^{-2}	**kg N ha^{-1}**
Two-row	**KWS Tower**	360	190
Six-row	**Volume**	270	190

3.2.2 Treatments

Two methods were used to assess the source-sink balance of the varieties. The first was an estimation of potential assimilate supply by measuring light interception by healthy tissue, biomass and stem storage reserves and comparing this to achieved yield as described by (Bingham et al., 2007a). The second method was by deliberately manipulating the assimilate availability per grain by imposing shading, row-opening and de-graining treatments 14 days post-anthesis.

The experimental design was a split-split plot design with four replicate blocks. Variety was randomised in the main plots, fungicide treatment in the subplots and source-sink manipulations in the sub-sub plots. Varieties were the same as those used in chapter two, KWS Tower (Tower) and Volume. Fungicide programmes applied were as follows; (1) untreated, (2) a four spray programme, with applications at GS 25, 31/32, 49 and 65. The products used reflected a commercial programme. The GS 25 timing used 0.4 l ha^{-1} of prothioconazole 250 g $litre^{-1}$ (Proline®, Bayer Crop Science, Monhem am Rhein, Germany) and 0.4 l ha^{-1} of fenpropimorph 750 g $litre^{-1}$ (Corbel®, BASF, Ludwigshafen, Germany). The GS31/2 and GS49 used 1.8 l ha^{-1} of epoxiconazole, 41.6 g $litre^{-1}$, fluxapyroxad 41.6 g $litre^{-1}$ and pyraclostrobin 66.6 g $litre^{-1}$ (Ceriax®, BASF, Ludwigshafen, Germany). The GS65 timing consisted of 0.4 l ha^{-1} prothioconazole g $litre^{-1}$ and 1 l ha^{-1} of chlorothalonil (CTL) 500 g $litre^{-1}$ (Bravo®, Syngenta, Basel, Switzerland). Fungicide was applied to each plot at a rate of 200 l ha^{-1} of water using a hand-held pressurised plot sprayer, using flat fan nozzles at 2 bar pressure.

At the sub-plot level, there were three adjacent plots of the same variety x fungicide treatment combination; the first was used for biomass sampling to estimate assimilate supply for grain filling, the second was used for source-sink manipulations, and the third was used for disease assessment and final harvest yield with a plot combine.

The manipulation treatments imposed in sub-sub plots were; shading, row-opening and de-graining. Row-opening and de-graining treatments were applied to both fungicide-treated and untreated plants, while shading was imposed on fungicide-treated plants only. This was to reduce the workload to manageable levels and focus the treatment on the most informative situation. It was anticipated that in the absence of disease (i.e. fungicide treated crops) six- and two-row varieties would differ in their degree of sink limitation. Reducing the

availability of assimilate by shading was expected to reduce grain filling to different extents in the two varieties. Thus, shading would be expected to highlight differences in sink limitation between ear types in disease-free crops. In diseased crops, on the other hand, both six- and two-row varieties may already be source-limited. Thus, reducing the amount of assimilate available for grain filling by shading would be expected to affect each ear type similarly and hence be less informative. Details of the manipulation treatments are given in 1.1.4 along with specific sampling and measurement procedures.

3.2.3 Disease and % green area assessment

The severity of foliar disease and the % of leaf area that was healthy (green) was assessed on ten shoots sampled at random from the designated combine plots at GS31, 39, 55, 55 plus two weeks and 55 plus four weeks. Shoots were pulled and placed into a labelled polythene bag and brought to the lab for assessment. If the assessment could not take place immediately, shoots were stored in a cold room (4-6°C) for no more than two days until assessment was carried out.

Individual foliar diseases were assessed on the top 3-4 fully expanded leaves. The foliar diseases assessed were; rhynchosporium leaf blotch (*Rhynchosporium commune)*, powdery mildew (*Blumeria graminis f. sp. hordei)*, ramularia leaf spot (*Ramularia collo-cygni)*, net blotch (*Pyrenophora teres)*, the spot form (*P. teres f. maculate*) and the net form (*P. teres f. teres*), brown rust (*Puccinia hordei*) and Septoria nodorum blotch (*Stagonospora nodorum*).

Percentage green area assessment was conducted on specific zones. Each zone consisted of the leaf lamina and the stem (plus leaf sheath) section above that leaf. Green area % was scored visually for both the laminae and the stem plus sheath in each zone. The ear comprised an additional zone and was also scored. Once visual assessment was completed, the absolute projected area (one surface only including healthy and senescent tissue) was measured for each fraction in each zone using a WD3 WinDIAS Leaf Image Analysis system (Delta-T devices, Cambridge, UK). The date of canopy senescence was recorded on a whole plot basis when <5% green area could be observed.

3.2.4 Photosynthetically active radiation interception

Interception of photosynthetically active radiation (PAR) was measured using a SunScan canopy analysis system (Delta-T Devices, Cambridge, UK) within three days of disease assessment. Measurements were conducted between the hours of 10:00 and 15:00 at 8 locations within each plot. Eight readings were taken per plot at a 45° angle to the row direction. Daily incident PAR was estimated as 0.5 x daily solar radiation (McCree, 1981) measured from the onsite weather station, within 1km of the trial location.

3.2.5 Biomass and absolute green area

Quadrat samples of 1.5m x 4 rows (0.75 m^2) were taken at GS31, 39, 55 and approximately weekly during grain filling. Samples were a minimum of 0.3m away from the plot edges and previous/future sample areas. Samples were representative of the entire plot and avoided drill overlaps, tractor wheelings, areas of compaction and tramlines. The plants within the sample areas were cut at ground level placed in polyethylene bags to prevent moisture loss and then brought to the lab for analysis. If growth analysis was delayed, samples were stored in a cold room (4-6°C) until processing took place. For the most part, analysis was completed within three days of sampling and never longer than five days. If the base of the shoots were contaminated with soil, this was removed by gently shaking or running them under a tap. Surface water was removed using a paper towel or by gently shaking prior to analysis. Samples were weighed fresh, then living shoots were separated into ten equal piles, each pile was weighed, and two subsamples were taken SS1 and SS2.

The first was a 20% sub-sample (SS1) based on weight and shoot number used for dry matter determination. The shoots were counted, then separated into the following sections; leaf lamina, stem plus leaf sheath, and ear (post GS 55). Each section was weighed fresh then oven-dried at 70°C for 48 hours, and dry weight was measured.

The second sub-sample (SS2) was a 10% sample based on weight for assessment of green area. The shoots were also counted, subsequently, the sample was divided into the following sections;

I. green leaf lamina,
II. non-green leaf lamina,
III. green stem,

IV.non-green stem,
V.green ear
VI.non-green ear

The green sections were then used for assessment of green area (one surface only), using a WD3 WinDIAS Leaf Image Analysis System (Delta-T Devices, Cambridge, UK). Each fraction was then oven-dried at 70°C for 48 hours and dry weight recorded. The samples were then placed in sealed polyethylene bags and stored.

A final sample was taken just prior to harvest for assessment of final biomass. Plants within 1.5m x 4 row quadrats were cut at ground level and placed spike first into polyethylene bags to ensure no spikes were lost. Samples were then transported and stored in a glasshouse on racks prior to growth analysis. Again, growth analysis was carried out within five days of sampling.

3.2.6 Determination of stem water-soluble carbohydrates (WSC)

Just prior to anthesis and approximately weekly during grain filling, 15 shoots were sampled per sampling plot for assessment of stem WSC. Whole shoots were sampled and placed in polyethylene bags and placed in a cold box (4-6°C) for transport to the lab. Once brought to the lab, samples were processed immediately. Roots were cut from the shoots, and the sample was weighed fresh, samples were then divided into leaf lamina, stem plus leaf sheath and ear. Samples were flash dried in a pre-heated oven at 110°C for 2 hours, then the temperature was reduced to 70°C for 48 hours. Each portion was weighed dry and stored in sealed plastic bags to await assessment of water-soluble carbohydrate.

Stem plus leaf sheath samples taken at anthesis, the time of maximum shoot dry weight and the time at which ear weight ceased to increase (considered to be the end of grain filling) were finely ground (< 2.0mm) in a cutting mill (RetschMühle, Retsch GmbH Haan, Germany). Once ground a sub-sample of approximately 30mg was taken and weighed to the nearest 0.1mg. Subsamples were extracted sequentially in 0.75ml 80% v/v ethanol:water, 50% ethanol and then deionized water at 60°C for 60 minutes. The extracts were evaporated to dryness in a centrifugal evaporator (miVac, Genevac LTD Ipswich England) at 70°C. Extracts were then re-suspended in 1.5ml of de-ionized water and the soluble sugar concentration determined colourimetrically using the phenol-sulphuric acid method (Dubois et al., 1956).

3.2.7 Source-sink manipulations and sampling

Source-sink manipulations were imposed two weeks after GS55. The timing was selected in order impose treatments after the period of endosperm cell number formation, which has been related to final grain weight (Cochrane and Duffus, 1981, Duffus and Cochrane, 1992). All manipulations were imposed on the same sub-plot area (Figure 3-1). In 2017 the date of fertilization was assessed by dissecting open spikelets of main shoot ears and recording when pollen was observed on the stigma (Waddington et al., 1983); this corresponded with GS55 and was closely followed (within a day or so) by extrusion of anthers (anthesis).

Shading

The shading material used was an open weave polystyrene shade-netting (Tildenet Ltd., Bristol, UK). Shades were 2 x 3m in size and were erected 0.5m above the crop canopy using the system described by (Kennedy et al., 2018). The shades were erected on wooden fencing posts using a rope frame as seen in (Figure 3-1) Shades were removed once the crop had reached physiological maturity (GS87).

An initial sample was taken for determination of biomass at the time of erecting the shading and a further sample immediately pre-harvest following the same procedures as the biomass sampling described above. A pyranometer (SPLite2, Kipp & Zonen B. V., Delft, Netherlands) and a relative humidity/temperature probe (MP100A, Rotronic Instruments (UK) Ltd., Crawley, UK) connected to a data logger (CR1000, Campbell Scientific Ltd., Loughborough, UK) were used to measure climatic conditions in shaded and un-shaded areas in one replicate only. Lodging (>45° from vertical), leaning (5-45° from vertical) and brackling (stem failure >1/3 from the base) assessment in previously shaded and un-shaded areas were conducted after shading treatments were removed.

De-graining

All ears along a 0.5m length of row were de-grained at two locations per plot. The top half of the ear was removed by pinching off grains and the upper rachis by hand without damaging the lower grains or the awns attached to these grains.

An initial 0.5m row length sample was taken at the imposition of the de-graining treatment at two locations per plot for assessment of biomass, biomass partitioning and stem WSC.

Shoots were cut at ground level, placed in polyethylene bags brought to the lab and processed immediately. The whole sample was weighed fresh, flash dried in the oven at 110°C for two hours and then at 70°C for the next 46 hours. Following drying, the whole sample was weighed, then divided into the following fractions; leaf, stem (plus leaf sheath), top and bottom ear halves and each faction weighed. Ears were halved using the same method as was implemented in the field.

Pre-harvest samples were taken at physiological maturity (GS87) 2 x 0.5m rows of de-grained and control shoots were cut at ground level, placed ear first into polyethylene bags and brought to the lab where they were processed following the same procedure used for initial samples. Control ears were divided into upper and lower halves for comparison with de-grained ears. Once ears were separated and dried, they were hand threshed between two pieces of foam board. Grain was cleaned using a winnower to remove awns and chaff, weighed and mean grain weight (MGW) was determined to the nearest 1 mg using a grain counter (Pfeuffer GmbH, Kitzingen, Germany) to count the number of grains in a sample of known dry weight.

Row-opening

Adjacent rows along a 3m long central row were pushed back using a system of white fencing stakes and bailing twine as seen in Figure 3-1. Rows were monitored regularly to ensure that the adjacent rows had not closed in.

The initial samples taken for the de-graining treatment (described above) served as initial samples for row-opening as they were in carried out in the same plot. At physiological maturity (GS87) the opened row was cut at ground level and placed ear first into polyethylene bags to avoid loss of material. The sample was brought to the lab, and immediately oven-dried at 110^{o}C and then 70^{o}C as described above. After recording the dry weight, a 40% subsample was taken by weight to facilitate further processing. Ears were divided into upper and lower halves for comparison with de-grained ears. Once ears were separated and dried, they were hand threshed between two pieces of foam board. Grain was cleaned using a winnrower, weighed and mean grain weight (MGW) was determined as described above.

The increase in light inception by the exposed row caused by row-opening was measured using a SunScan Canopy Analysis System at GS55 (Delta-T devices, Cambridge, UK). The lance of the device was placed along an unopened row of plants, the incident PAR and PAR transmitted to the base of the canopy was simultaneously measured five times. Plants were removed along the length of the lance, incident and transmitted PAR was re-measured five times again. The number of shoots removed was recorded. This procedure was repeated for a row that was opened and for each variety. These were replicated measurements made on a single plot each of variety Tower and Volume.

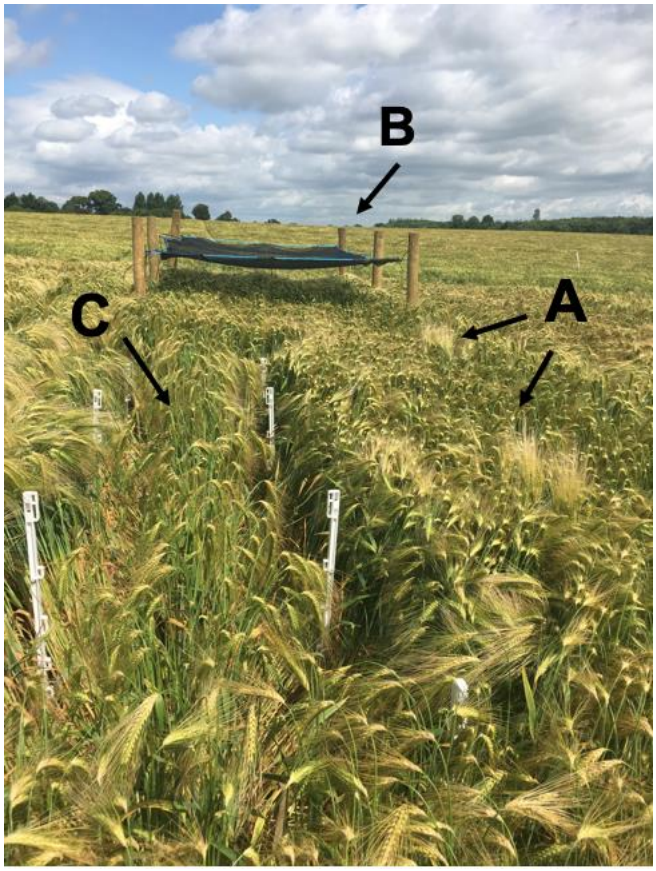

Figure 3-1. Manipulation plot. A) de-graining, B) shading and C) row-opening.

Stem WSC were determined on shoots sampled from the manipulation treatments at the time of treatment imposition and at grain physiological maturity (pre-harvest) as described above.

3.2.8 Combine harvest

Plots assigned for combine harvesting were cut using a Sampo 2010 plot combine (Sampo Rosenlew Ltd Konepajanranta 2, PORI FINLAND). Moisture, hectolitre weight (HTW) and plot weight were obtained using Harvest Mater classic Grain Gauge (Juniper Systems, Inc., 1132 W 1700 N, Logan, UT, 84321, U.S.A). Plot yield was corrected to t ha^{-1} and 100% dry matter. A ~1kg grain sample was taken from each plot for assessment of MGW as described above. The number of grains m^{-2} was calculated as combine yield divided by MGW and corrected to 85% dry matter.

3.2.9 Calculations and statistical analysis

Photosynthetically active radiation (PAR) interception by healthy tissue was estimated using the method described by (Bingham et al., 2019). Canopy area index was calculated from a canopy light extinction coefficient (k) of calculated using equation 1 for assessments at GS31, 39 55 and GS 55+2 weeks and an assumed value was used at GS 55+4 weeks of -0.6 and from the measured value of fractional PAR transmission.

$$Kpar = \frac{\ln\left(\frac{I}{I_0}\right)}{GAI} \qquad 1)$$

Where *Io* is the incident Par and I is the PAR transmitted to the base of the canopy and GAI

$$CAI = \frac{Ln\left(\frac{I}{I_0}\right)}{-k} \qquad 2)$$

Where I_0 is the incident PA,R and I is the PAR transmitted to the base of the crop.

The fractional distribution of projected area from the measured samples was used to estimate the CAI in each layer as equation 3

$$CAI_h = CAI \text{ x } fLA_h \qquad 3)$$

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.

The daily PAR interception by each zone in the canopy at a given growth stage was then estimated using beer's law analogy as:

$$I_h = I_{oh} \times \left[1 - exp^{(-k \times CAIh)}\right] \qquad 4)$$

Where I_h is the PAR interception by layer h on a given day, I_{oh} is the daily PAR incident on that layer and CAI_h is the area index of the canopy in layer h. I_{oh} is 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 the layers above layer h. The PAR intercepted by green tissue in a given layer H was given as:

$$HAint_h = I_h \times \frac{HAI_h}{CAI_h} \qquad 5)$$

Where $HAint_h$ is the green area PAR interception by layer *h* and HAI_h/CAI_h is the fraction of the area index in layer*h* that is green (healthy). H was calculated from a weighted averaged of the measured % green area values of leaf lamina and stem plus leaf sheath for the layer in question, apart from the ear which was calculated from the % green area on the ear alone.

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 ($I_o\ day$)

$$F_{PAR} = \frac{HAint}{I_{o\ day}} \qquad 6)$$

F_{PAR} was then interpolated for the days in between each sampling date and total intercepted PAR calculated from daily values of incident PAR data multiplied by F_{PAR}. 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 not reflected or transmitted to neighbouring green healthy tissue

Estimation of assimilate supply was then calculated from a modified method as described by Bingham et al., (2007a). Radiation use efficiency (RUE) was determined by plotting cumulative PAR interception by healthy tissue against the cumulative increase in above-ground biomass from destructive sampling from GS31. Potential assimilate supply available for grain filling was then calculated using equation 7.

$$\text{(Post-anthesis HAint x RUE) + WSC} \qquad 7)$$

Where WSC is the amount of water-soluble carbohydrates in the stem at anthesis expressed at 100% dry matter. The potential post-anthesis assimilate supply plus the weight of grains at anthesis (prior to grain filling) gave the potential yield. This husk weight was measured from both fungicide treated and untreated ears of both varieties at GS55. The estimated mean grain weight in the absence of sink limitation was then calculated as the potential yield

divided by grains m^{-2} obtained from combine harvest plots. The % utilisation of WSC was calculated as the difference in the amount of WSC between the time of anthesis and the end of grain filling, expressed as a % of the former.

In 2016 absolute area for leaf and stem was carried out together for each zone at GS39 only, while there was individual assessment of % green area conducted. To get a weighted % green area for the zone the ratio of stem: leaf for each zone was calculated from 2017 GS39 absolute area measurements for each variety. This ratio was then used to calculate the area of stem and leaf in 2016 at GS39.

Row-opening reduces the amount of shading the target row receives from adjacent plants and thereby increases the transmission of PAR through the canopy and the amount intercepted by the exposed row. The increase in light interception was calculated as follows. Firstly, the PAR interception by plants within a designated unopened row was estimated as the fraction of PAR interception before plant removal minus that after plant removal. The fraction of PAR intercepted by plants in a designated opened-row was similarly calculated. After converting to absolute amounts of PAR interception using a common value of incident PAR, the difference in PAR interception with and without row opening was estimated. These calculations indicate a 45% and 10% increase in the amount of light intercepted per row in Tower and Volume receptively

All statistical analyses were carried out using GenStat (18^{th} Edition, VSN International Ltd., Hemel Hempstead, UK). Normality was checked using a probability of distribution test in GenStat, while homogeneity was checked using bartlett's test.

The effect of variety and fungicide on the potential yield was analysed using a split-plot ANOVA model where variety and fungicide treatment was investigated in the fixed model for each year individually. Replicate was included in the blocking structure.

The effects of manipulations and fungicide treatment on MGW and % WSC utilised during grain filling in both varieties were analysed using a split-split plot ANOVA model where variety, fungicide treatment and source-sink manipulation was investigated in the fixed model for each year individually. Replicate was included in the blocking structure. % WSC utilised was arcsine transformed in Microsoft Excel® 2010. Values presented in results are back-transformed.

Climatic conditions under and outside the shaded area were recorded every hour. Daily average temperature, relative humidity (RH) and total daily incident PAR was calculated for a two week period during treatment in 2016 only as the battery powering the data logger ran out in 2017 and data were lost. The effect of shading on the climatic conditions was then analysed using a two-way ANOVA with day as the unit of replication.

3.3 Results

3.3.1 Meteorological data

The growing season is defined as the period between from October to July. Long term (1981-2010) average total rainfall was 699 mm for the growing season, while average temperature during the same period was 8.9 °C. Solar radiation at Teagasc had a seasonal average of 2698 MJ m^{-2} in the period from 2008-2014. The 2016 season was wetter and warmer than the long term average. The average temperature was 9.6°C for the 2016 season (Figure 3-3), and rainfall totalled 902 mm for the season, although this was mainly caused by an extremely wet month of December in which rainfall was 124% higher than normal (Figure 3-2). Conversely, the 2017 season was drier than normal with total rainfall of 528 mm for the season (Figure 3-2), while temperature again as higher (9.3°C) than the long term average (Figure 3-3). The level of solar radiation experienced in 2016 was similar to normal (accumulated radiation = 2638 MJ m^{-2}), following a similar trend to average values, although the radiation in May was above normal while radiation in June was lower than average (Figure 3-4). The solar radiation in 2017 was above normal (accumulated radiation = 2638 MJ m^{-2}), values for March and May were above average, while values for April were below normal (Figure 3-4).

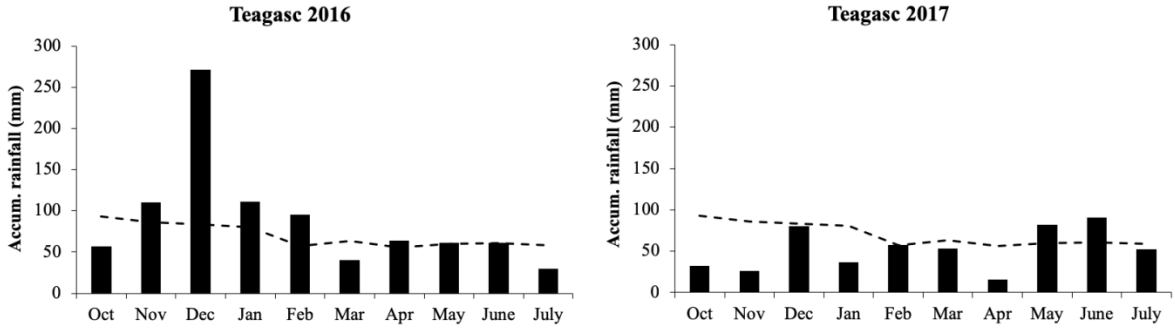

Figure 3-2. Monthly accumulated rainfall (mm) from October to July for both years. Broken lies are long-term mean values (1981-2010) for each year.

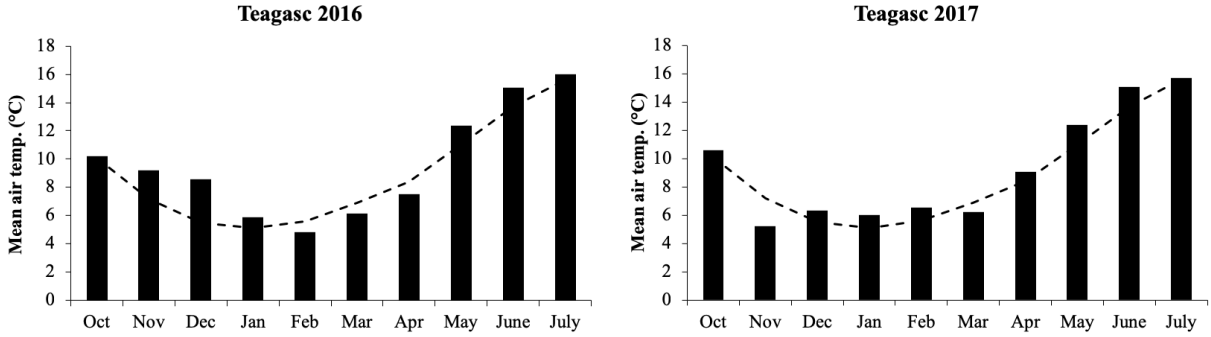

Figure 3-3. Monthly mean temperatures (°C) from October to July for both years. Broken lies are long-term mean values (1981-2010) for each year.

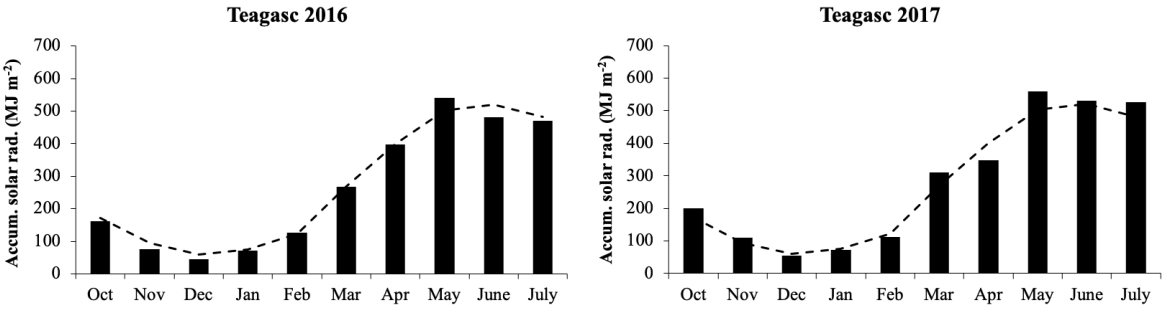

Figure 3-4. Monthly accumulated solar radiation (MJ m^{-2}) from October to July for both years. Broken lies are long-term mean values (1981-2010) for each year.

3.3.2 Disease pressure and spectrum

The severity of disease averaged over the top three leaves is presented in Table 3-2. In 2016 at GS31 and GS39 Septoria nodorum (1-2%) and powdery mildew dominated (4-6%). At GS55 again Septoria nodorum and mildew were present with some low levels of brown rust (>1%). In an assessment carried out at GS55 + two weeks, ramularia, Septoria nodorum, and mildew were the main diseases present (Figure 3-5). In 2017 mildew was the main disease present at GS31, GS39 and GS55. At GS55 + two weeks ramularia and mildew were the main diseases in both varieties (Figure 3-6), although there was also some spot form of net blotch in Tower.

At no assessment was there a difference between varieties in the severity of disease observed ($p>0.05$) (Table 3-2). The untreated programme had significantly more disease compared to the treated ($p<0.05$), with the exception of the GS39 assessment in 2016 and GS31 assessment in 2017 where no difference was observed. Only at one assessment, GS31 in 2016, was the variety x fungicide interaction significant ($p>0.05$) although the level of disease was very low.

Table 3-2. Effects of variety and fungicide on the total severity of all disease averaged over the top three leave for GS31, GS39 and GS55 while GS55+2 was top two leaves. Means and P- values (back-transformed) from values produced by ANOVA analysis.

2016					
Variety	**Fungicide**	**GS31**	**GS39**	**GS55**	**GS55+2 weeks**
Tower	**Untreated**	0.73	2.59	5.52	20.67
Tower	**4 spray**	0.15	1.17	1.47	3.57
Volume	**Untreated**	0.26	2.43	5.65	26.26
Volume	**4 spray**	0.22	2.17	1.76	3.46
Variety mean	**Tower**	0.44	1.88	3.50	12.12
	Volume	0.24	2.30	3.70	14.86
Fungicide mean	**Untreated**	0.19	1.67	1.62	23.46
	4 spray	0.49	2.51	5.59	3.51
Significance	**df**	P	P	P	P
Variety (V)	**1**	0.149	0.602	0.636	0.367
Fungicide (F)	**1**	0.006	0.129	<.001	0.007
V*F	**1**	0.013	0.254	0.76	0.688
2017					
Variety	**Fungicide**	**GS31**	**GS39**	**GS55**	**GS55+2 weeks**
Tower	**untreated**	2.06	0.40	1.97	24.36
Tower	**4 spray**	2.57	0.85	0.10	0.65
Volume	**untreated**	1.60	0.26	3.10	24.34
Volume	**4 spray**	2.80	0.81	0.28	0.88
Variety mean	**Tower**	2.31	0.62	1.03	12.51
	Volume	2.20	0.54	1.69	12.61
Fungicide mean	**untreated**	1.83	0.33	0.19	24.35
	4 spray	2.68	0.83	2.53	0.77
Significance	**df**	P	P	P	P
Variety (V)	**1**	0.847	0.291	0.095	0.741
Fungicide (F)	**1**	0.256	<.001	<.001	<.001
V*F	**1**	0.628	0.313	0.643	0.737

The residual d.f were 3 and 6 for the main plot and sub-plot respectively.

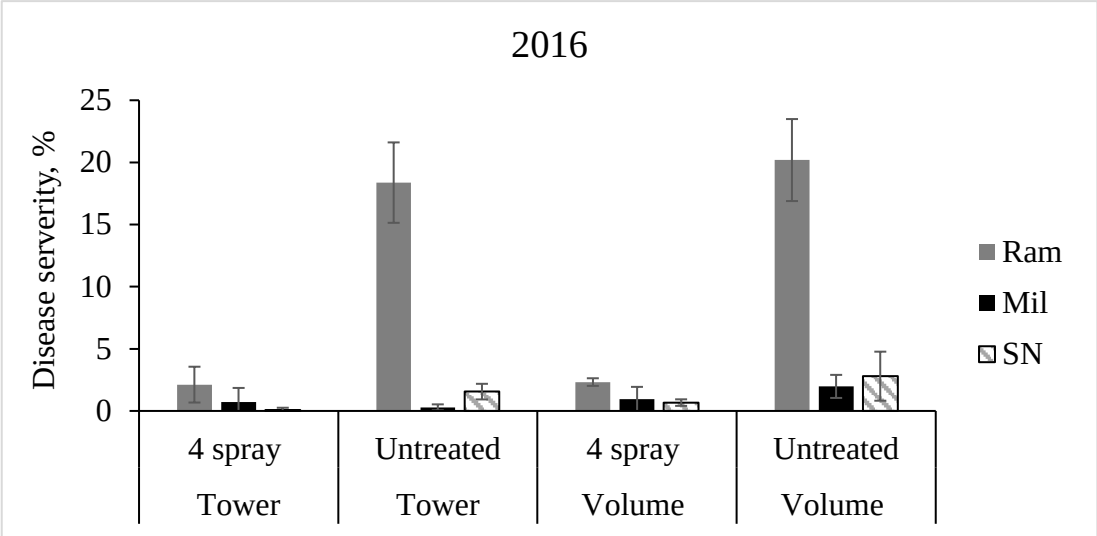

Figure 3-5. The effect of variety and fungicide treatment on the severity of ramularia (Ram), powdery mildew (Mil) and Septoria nodorum (SN) averaged over leaf 1 & 2 at GS 55 + 2 weeks in 2016 where flag leaf is leaf 1. Values presented are back-transformed from means produced by ANOVA analysis on arcsine transformed data. Error bars represent the standard error of the mean.

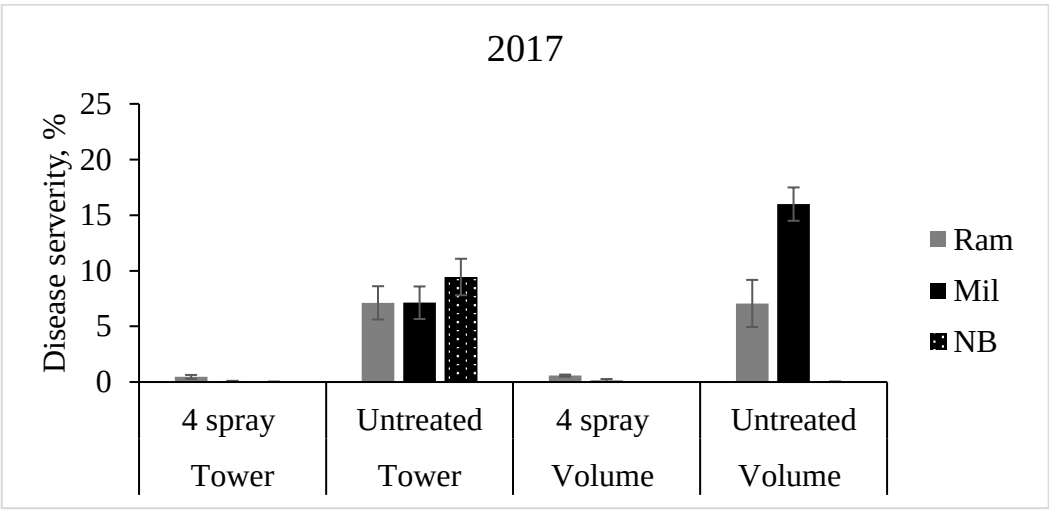

Figure 3-6. The effect of variety and fungicide treatment on the level of ramularia (Ram), powdery mildew (Mil) and spot for of net blotch (NB) on an average of leaf 1, & 2 at GS 55 + 2 weeks in 2017. Values presented are back-transformed from means produced by ANOVA analysis on arcsine transformed data. Error bars represent the standard error of the mean.

3.3.3 Effect of fungicide treatment on yield

Fungicide treatment increased yield by 46% and 38% for Tower and Volume respectively in 2016, while in 2017 the effect was larger with yield increases of 127% and 83% for Tower and Volume respectively when to the untreated treatment ($p<0.05$) (Table 3-3). Averaged across fungicide treatments, the yield of both Volume and Tower was similar ($p>0.05$). The increase in yield with fungicide was the result of an increase in both the number of grains m^{-2} and the MGW. In 2016 the variety x fungicide interaction was significant for grains m^{-2}, caused by the increase from fungicide treatment being larger in Volume compared to Tower ($p<0.05$). In 2017 this interaction was not significant, although fungicide treatment did increase grains m^{-2} significantly when averaged over both varieties ($p<0.05$). In both years Volume produced 20% and 15% more grains m^{-2} compared to Tower in 2016 and 2017 respectively. In both 2016 and 2017 fungicide treatment increased MGW to a greater extent in Tower (16-17%) than in Volume (4-6%), leading to a significant variety x fungicide interaction ($P<0.05$). MGW was lower in Volume than Tower in each of the fungicide treatments ($p<0.05$) offsetting the contribution to yield of its larger number of grains m^{-2}.

Table 3-3. Effects of treatments on the yield, mean grain weight (MGW) (at 100% dry matter) and grains m^{-2} for both years. Means, P and LSD values presented were produced by ANOVA analysis.

		Yield (t ha^{-1})				Grains m^{-2}				MGW (mg)			
Variety	**Fungicide**	**2016**		**2017**		**2016**		**2017**		**2016**		**2017**	
Tower	**4 spray**	8.36		8.02		18794		18898		44.48		43.31	
Tower	**Untreated**	5.69		3.54		15045		9755		37.88		37.40	
Volume	**4 spray**	8.73		8.04		25716		23066		33.95		34.81	
Volume	**Untreated**	6.35		4.39		19833		14267		31.99		32.72	
Variety mean	**Tower**	7.03		5.78		16919		14327		41.18		40.36	
	Volume	7.21		5.79		20381		16411		35.92		36.11	
Fungicide mean	**4 spray**	8.55		8.03		22255		20982		39.22		39.06	
	untreated	6.02		3.97		17439		12011		34.94		35.06	
Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.161	ns	0.406	ns	0.008	2936	0.022	3175	<0.001	1.78	0.028	5.26
Fungicide (F)	**1**	<0.001	0.51	<0.001	0.83	<0.001	987	<0.001	2393	0.002	1.82	0.002	1.47
V*F	**1**	0.503	ns	0.265	ns	0.039	2759	0.867	ns	0.022	2.08	0.022	5.03

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

3.3.4 Potential assimilate supply.

In both years there was no significant difference between varieties in the level of PAR interception by healthy tissue during the pre-anthesis period (GS31-55) ($p<0.05$), while the same was true for fungicide programmes with the untreated and 4 spray programmes incepting similar levels of PAR in 2017, however in 2016 fungicide treatment increased pre-anthesis PAR interception by health tissue, although this difference was small ($p = 0.025$) (Figure 3-7).

There was 59% more WSC present in the stems at anthesis of Tower compared to Volume in 2016 ($p<0.05$) and 21% more in 2017 ($p=0.079$). This was due to a difference in stem weight at anthesis rather than concentrations of WSC in the tissue (Table 3-4). Fungicide treatment did not affect the amount of WSC present in the stems at anthesis in either year ($p>0.05$) (Table 3-4).

Fungicide treatment increased post-anthesis PAR interception by healthy tissue in both Tower and Volume. In 2016, the scale of the effect was comparable in each variety. In 2017 PAR interception by untreated crops was greater in Volume than Tower and the increase with fungicide treatment smaller, thus giving rise to significant variety x fungicide interaction ($p<0.05$) (Table 3-5). This effect was largely due to greater retention of green area in Volume compared to Tower (data not presented). Averaged across fungicide treatments Volume intercepted 7% more PAR by healthy tissue during the grain filling period compared to Tower in 2016 and 13% more in 2017 ($p<0.05$).

In general, effects of fungicide treatment on RUE were smaller than those on healthy area PAR interception (Table 3-5). In 2016 there was no overall effect ($p>0.05$) of fungicide treatment or variety on RUE, but there was a significant variety x fungicide interaction ($p<0.05$). RUE of fungicide treated Tower was greater than that of untreated controls, whereas in Volume it was marginally lower. In 2017, fungicide treatment increased RUE in both Tower and Volume, but to a greater extent in Tower resulting again in a significant variety x fungicide interaction ($p<0.05$). As in 2016, there was no overall effect of variety on RUE.

In both 2016 and 2017 fungicide treatment decreased the % utilisation of WSC during grain filling ($p<0.05$). The interaction between variety and fungicide was not significant in either year ($p>0.05$) and there was no overall effect of variety.

Fungicide treatment significantly increased estimates of potential yield by 43% and 61% in 2016 and 2017 respectively ($p<0.05$) when averaged over varieties (Table 3-6). Varieties differed in their response to fungicide. Fungicide increased potential yield to a greater extent in Tower compared to Volume in both 2016 and 2017 (variety x fungicide, $p<0.05$). There was no significant overall difference between varieties in their potential yield ($p<0.05$) in either year. There was no significant effect of variety or fungicide treatment on the difference between the potential yield and actual yield (Table 3-6). In 2016 the estimated potential yield was lower than the measured yield, although the balance was close with the average difference across treatments being 0.8 t ha^{-1}. In 2017 potential yield was considerably larger than the actual yield with the average difference across treatments being 2.1 t ha^{-1}. The 95% confidence interval for the difference between potential and measured yield in 2016 was -3 t ha^{-1} to 1.9 t ha^{-1}, whilst in 2017 it ranged from 1 to 2.8 t ha^{-1}.

Table 3-4. Effect of variety and fungicide on the amount of water-soluble carbohydrates (WSC) (g m^{-2}), stem weight (g $shoot^{-1}$) and WSC concentration (conc.) at anthesis. Means, P and LSD values presented were produced by ANOVA analysis. Means for WSC conc. % at anthesis presented are back-transformed from values produced by ANOVA analysis on arcsine transformed data.

		WSC at anthesis g m^{-2}		**Stem weight per shoot**		**WSC conc. % at anthesis**	
Variety	**Fungicide**	**2016**	**2017**	**2016**	**2017**	**2016**	**2017**
Tower	**4 spray**	125.24	100.90	0.63	0.68	14.96	12.61
Tower	**Untreated**	101.44	101.02	0.60	0.72	13.33	12.81
Volume	**4 spray**	76.85	87.42	0.80	0.93	10.60	12.28
Volume	**Untreated**	66.04	79.47	0.88	0.91	9.71	12.94
Variety mean	**Tower**	113.34	100.96	0.61	0.70	14.14	12.71
	Volume	71.45	83.45	0.70	0.82	11.96	12.54
Fungicide mean	**4 spray**	101.05	94.16	0.72	0.80	12.78	12.44
	Untreated	83.74	90.25	0.74	0.81	11.52	12.88

Significance	**df**	P	LSD	P	LSD	P	LSD	P	LSD	P	P
Variety (V)	**1**	0.049	41.46	0.074	ns	0.002	0.067	0.003	0.082	0.068	0.87
Fungicide (F)	**1**	0.071	ns	0.694	ns	0.558	ns	0.725	ns	0.085	0.758
V*F	**1**	0.442	ns	0.685	ns	0.139	ns	0.31	ns	0.652	0.869

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

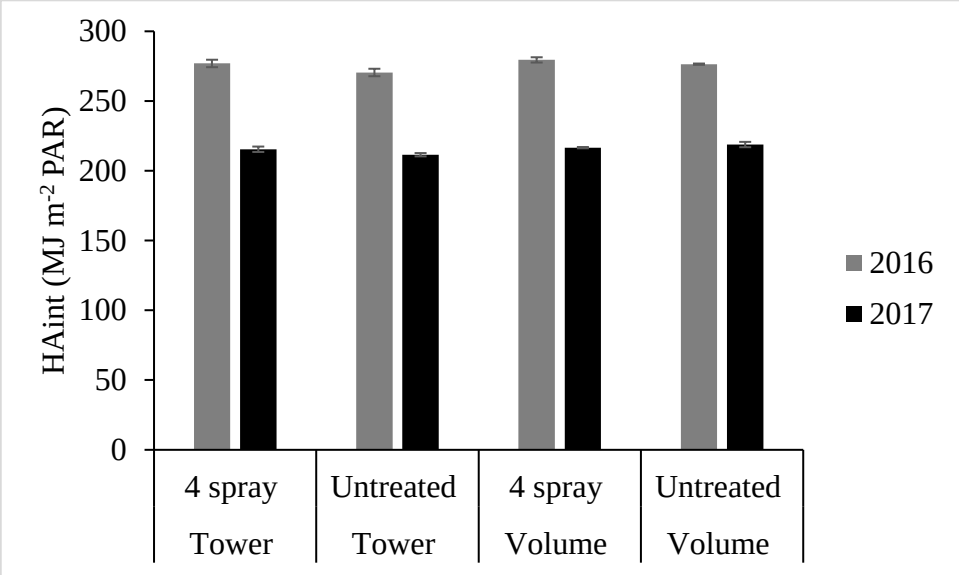

Figure 3-7. Effect of variety and fungicide treatment on the amount of PAR intercepted by healthy tissue (HAint) during the pre-anthesis period (GS31-55). Error bars represent the standard error of the mean.

Table 3-5. Effects of treatments on post-anthesis PAR interception by healthy tissue (HAint), radiation use efficiency (RUE)and % water-soluble carbohydrate (WSC) utilisation . Means, P-values and LSD's presented from values produced by ANOVA analysis. Means for WSC conc. % at anthesis presented are back-transformed from values produced by ANOVA analysis on arcsine transformed data.

		Post anthesis HA int		**RUE**		**% WSC Utilisation**	
Variety	**Fungicide**	**2016**	**2017**	**2016**	**2017**	**2016**	**2017**
Tower	**Treated**	226.9	315.8	2.49	2.68	82.6	91.2
Tower	**untreated**	148.8	199.2	2.22	2.04	90.6	96.8
Volume	**Treated**	231.8	328.2	2.52	2.42	88.8	92.3
Volume	**untreated**	173.6	258.1	2.65	2.21	92.3	96.4
Variety Mean	**Tower**	187.9	257.5	2.36	2.36	86.6	94.0
	Volume	202.7	293.1	2.59	2.32	90.6	94.4
Treatment mean	**Control**	229.4	322.0	2.51	2.55	85.7	91.8
	Treated	161.2	228.6	2.44	2.13	91.5	96.6

Significance	**df**	P	LSD	P	LSD	P	LSD	P	LSD	P	P
Variety (V)	**1**	0.019	10.2	0.038	31.9	0.082	ns	0.351	ns	0.197	0.944
Fungicide (F)	**1**	<.001	14.3	<.001	18.2	0.355	ns	<.001	0.12	0.003	0.012
V*F	**1**	0.14	ns	0.021	30.3	0.027	0.28	0.004	0.14	0.2	0.66

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 3-6. Effect of variety and fungicide treatment on the potential yield, actual yield (100% dry matter) and the difference between the two. Means, P and LSD values presented were produced by ANOVA analysis.

		Potential yield (t ha^{-1})				Measured yield (t ha^{-1})				Difference			
Variety	**Fungicide**	**2016**		**2017**		**2016**		**2017**		**2016**		**2017**	
Tower	**4 spray**	7.76		10.35		8.36		8.02		-0.60		2.33	
Tower	**Untreated**	4.94		5.47		5.69		3.54		-0.75		1.94	
Volume	**4 spray**	7.45		9.59		8.73		8.04		-1.28		1.54	
Volume	**Untreated**	5.69		6.92		6.35		4.39		-0.60		2.53	
Variety Mean	**Tower**	6.35		7.91		7.03		5.78		-0.68		2.14	
	Volume	6.57		8.26		7.54		6.22		-0.94		2.04	
Treatment mean	**4 spray**	7.61		9.97		8.55		8.03		-0.94		1.94	
	Untreated	5.32		6.20		6.02		3.97		-0.68		2.24	
Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.240	ns	0.454	ns	0.161	ns	0.406	ns	0.479	ns	0.818	ns
Fungicide (F)	**1**	<0.001	0.28	<0.001	0.41	<0.001	0.51	<0.001	0.83	0.296	ns	0.500	ns
V*F	**1**	0.003	0.45	<0.001	1.18	0.503	ns	0.265	ns	0.130	ns	0.143	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

3.3.5 Source-sink manipulations

De-graining

Comparing the total number of grains ear^{-1} in the control and de-grained ears at harvest showed that on average there was a 43% reduction in grains ear^{-1} after de-graining, with a range of 30%-58% (data not presented).

Averaged across variety and fungicide treatments de-graining increased MGW of the remaining grains by 7.6% in 2016 ($p<0.01$) and 8.3% in 2017 ($p<0.05$). The variety x manipulation interaction was not significant for MGW in de-grained ears ($p>0.05$) in either year (Table 3-7). The fungicide x manipulation interaction was also not significant ($p>0.05$), while fungicide significantly increased MGW in both years ($p<0.05$). Tower had a significantly higher MGW compared to Volume ($p<0.05$). Importantly these values are from marked de-grained and control areas of 2 x 0.5 m rows, thus these values may be higher than total plot estimates presented in Table 3-3.

De-grained ears utilised a smaller % of WSC reserves during grain filling compared to no de-grained ears in both years ($p<0.05$), but the scale of the response differed between varieties and fungicide treatments (Table 3-7). The variety x manipulation for the level of WSC utilised during grain filling was significant in 2016 but not in 2017. This resulted from a smaller response to de-graining in Tower compared to Volume ($p<0.05$). The interaction between fungicide and manipulation was significant in both years ($p<0.05$). Untreated de-grained ears utilised a larger % of WSC during grain filling compared to fungicide treated de-grained ears ($p<0.05$), while in controls utilisation of WSC was comparable in fungicide-treated and untreated plants when the crop was fungicide treated. There was no significant difference between fungicide programmes in % WSC utilisation in 2016, while in 2017 a larger % of WSC was utilised when the crop was not treated with fungicide ($p<0.05$).

Row opening

The opening up of a row significantly increased MGW in both the top and bottom half of the ear in each year (4-10%) ($p<0.05$) (Table 3-8 and Table 3-9). The variety x manipulation interaction not significant in 2016 for both halves of the ear, although in 2017 it was significant for the bottom half of the ear. Here row-opening increased MGW in Tower

($p<0.05$) but not in Volume ($p>0.05$) (Table 3-8). The fungicide x manipulation interaction was not significant for each half of the ear in 2016 while in 2017 the interaction was significant for the top half of the only. In this case, row-opening significantly increased MGW in Tower when treated with fungicide ($p<0.05$), but had little or no effect in Volume or when Tower was not treated with fungicide. Averaged over other treatments fungicide treatment increased MGW in both years and both halves of the ear ($p<0.05$) and Tower had a higher MGW compared to Volume ($p<0.05$).

There was less WSC utilised when the crop was opened up compared to controls in both years ($p<0.05$) (Table 3-8 and Table 3-9). The response to row opening was comparable between varieties (variety x manipulation $p>0.05$) but was influenced by fungicide treatment in 2017. There was a significantly greater % of WSC utilised when the crop was not treated with fungicide ($p<0.05$) in 2017. The fungicide x manipulation interaction was not significant in 2016 ($p>0.05$). Averaged across other treatments, fungicide treatment decreased % WSC utilisation in both row-opened and controls in 2017 but not 2016, (Table 3-8). There was no overall difference in % WSC utilisation between varieties ($p>0.05$).

Shading

Shading reduced the amount of PAR which the crop could intercept by 75% ($p<0.05$) (Table 3-10). Shading of the crop did not significantly affect the relative humidity above the canopy ($p>0.05$), while the air temperature was just 0.1^{o}C lower under the shade ($p<0.05$).

Shading reduced MGW by 9.5% in 2016 and 11.5% in 2017 compared to controls ($p<0.05$) (Table 3-11). The variety x manipulation interaction was not significantly for MGW when the crop was shaded in either year ($p>0.05$)). MGW was significantly greater in Tower compared to Volume in both years ($p<0.05$) when averaged over shading treatments.

In 2017 a significantly greater % of WSC was utilised when the crop was shaded compared to unshaded ($p<0.05$). In 2016 the response to shading differed between varieties (variety x manipulation interaction $p<0.05$) as shading increased the % utilisation relative to controls in Tower, but not Volume. Averaged over all treatments, Volume utilised a greater % of WSC during grain filling compared to Tower in 2017 only ($p<0.05$).

Table 3-7. Effects of fungicide treatment and post-anthesis de-graining on mean grain weight (MGW (mg)) at 100% dry matter and water-soluble carbohydrates (WSC) utilisation. Means, P values and LSD produced from ANOVA analysis. Means for % WSC utilisation presented are back-transformed from values produced by ANOVA analysis on arcsine transformed data.

			MGW		% WSC utilisation	
Variety	**Fungicide**	**Manipulation**	**2016**	**2017**	**2016**	**2017**
Tower	**4 spray**	**Control**	49.97	53.05	94.2	92.8
Tower	**4 spray**	**De-grain**	53.06	58.20	78.4	56.4
Tower	**Untreated**	**Control**	41.19	41.38	93.1	94.0
Tower	**Untreated**	**De-grain**	45.02	46.27	91.9	92.7
Volume	**4 spray**	**Control**	34.52	43.59	96.3	93.8
Volume	**4 spray**	**De-grain**	37.91	46.12	68.2	58.2
Volume	**Untreated**	**Control**	33.59	39.18	94.3	92.1
Volume	**Untreated**	**De-grain**	36.05	41.46	79.5	88.3
Variety Mean	**Tower**		47.31	49.73	89.4	84.0
	Volume		35.52	42.59	84.6	83.1
Fungicide mean	**4 spray**		43.87	50.24	84.3	75.3
	Untreated		38.96	42.07	89.7	91.8
Manipulation mean	**Control**		39.82	44.30	94.5	93.2
	De-grain		43.01	48.01	79.5	73.9

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**P**
Variety (V)	**1**	0.002	3.52	0.002	2.24	0.223	0.521
Fungicide (F)	**1**	<.001	1.11	<.001	2.96	0.155	0.002
Manipulation (M)	**1**	0.001	1.62	0.024	2.18	<.001	<.001
V*F	**1**	<.001	3.30	0.003	3.18	0.587	0.378
V*M	**1**	0.727	ns	0.214	ns	0.004	0.652
F*M	**1**	0.944	ns	0.899	ns	0.003	<.001
V*F*M	**1**	0.587	ns	0.999	ns	0.701	0.691

The residual d.f were 3, 6 and 12 for the main plot, sub-plot and sub-sub plot respectively

Table 3-8. Effects of fungicide treatment and post-anthesis row-opening (RO) in the top half of the ear on mean grain weight (MGW (mg)) at 100% dry matter and water-soluble carbohydrates (WSC) utilisation. Means, P values and LSD produced from ANOVA analysis. Means for % WSC utilisation presented are back-transformed from values produced by ANOVA analysis on arcsine transformed data.

			MGW		% WSC utilisation	
Variety	**Fungicide**	**Manipulation**	**2016**	**2017**	**2016**	**2017**
Tower	**Trt**	**Control**	43.86	46.63	93.2	92.7
Tower	**Trt**	**Treated**	47.54	51.68	85.2	81.5
Tower	**Untrt**	**Control**	36.99	39.53	94.1	94.0
Tower	**Untrt**	**Treated**	39.36	39.79	94.5	92.9
Volume	**Trt**	**Control**	33.17	41.29	95.7	93.2
Volume	**Trt**	**Treated**	37.64	42.41	90.6	84.2
Volume	**Untrt**	**Control**	31.37	38.91	95.1	92.7
Volume	**Untrt**	**Treated**	35.58	39.11	91.7	91.5
Variety Mean	**Tower**		41.94	44.41	91.7	90.3
	Volume		34.44	40.43	93.3	90.4
Fungicide mean	**4 spray**		40.55	45.50	91.2	87.9
	Untreated		35.83	39.34	93.8	92.8
Manipultion mean	**Control**		36.35	41.59	94.5	93.2
	Treated		40.03	43.25	90.5	87.5

Significance	**df**	P	LSD	P	LSD	P	P
Variety (V)	**1**	0.003	2.83	0.039	3.59	0.64	0.94
Fungicide (F)	**1**	<.001	1.79	<.001	2.07	0.285	0.012
Manipultion (M)	**1**	<.001	1.82	0.008	1.24	0.012	<.001
V*F	**1**	0.009	2.73	0.013	3.41	0.304	0.298
V*M	**1**	0.447	ns	0.105	ns	0.602	0.666
F*M	**1**	0.647	ns	0.027	2.23	0.106	<.001
V*F*M	**1**	0.759	ns	0.115	ns	0.302	0.676

The residual d.f were 3, 6 and 12 for the main plot, sub-plot and sub-sub plot respectively

Table 3-9. Effects of fungicide treatment and post-anthesis row-opening (RO) in the bottom half of the ear on mean grain weight (MGW (mg)) at 100% dry matter. Means, P values and LSD produced from ANOVA analysis.

			MGW (mg)	
Variety	**Fungicide**	**Manipulation**	**2016**	**2017**
Tower	**4 spray**	**Control**	43.86	46.63
Tower	**4 spray**	**RO**	47.54	51.68
Tower	**Untreated**	**Control**	36.99	39.53
Tower	**Untreated**	**RO**	39.36	39.79
Volume	**4 spray**	**Control**	33.17	41.29
Volume	**4 spray**	**RO**	37.64	42.41
Volume	**Untreated**	**Control**	31.37	38.91
Volume	**Untreated**	**RO**	35.58	39.11
Variety Mean	**Tower**		41.94	44.41
	Volume		34.44	40.43
Fungicide mean	**4 spray**		40.55	45.50
	Untreated		35.83	39.34
Manipulation mean	**Control**		36.35	41.59
	Treated		40.03	43.25

Significance	**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.003	2.83	0.039	3.59
Fungicide (F)	**1**	<0.001	1.79	<0.001	2.07
Manipulation (M)	**1**	<0.001	1.82	0.008	1.24
V*F	**1**	0.009	2.73	0.013	3.41
V*M	**1**	0.447	ns	0.105	ns
F*M	**1**	0.647	ns	0.027	2.23
V*F*M	**1**	0.759	ns	0.115	ns

The residual d.f were 3, 6 and 12 for the main plot, sub-plot and sub-sub plot respectively

Table 3-10. Effects of shading on the meteorological environment beneath and outside the shade. P-Values were produced from two-way ANOVA analysis.

		Average daily PAR	Average daily RH	Average daily Temp.
Treatment		**MJ m^{-2}**	**%**	**C**
Shaded		3.6	85.3	13.3
Unshaded		14.3	85.2	13.4
Difference %		-74.6	0.2	-1.1
significance	***df***	P-Value	P-Value	P-Value
Residual	**13**	<0.001	0.612	0.016

Table 3-11. Effects of post-anthesis shading on mean grain weight (MGW (mg)) at 100% dry matter and water-soluble carbohydrates (WSC) utilisation. Means, P values and LSD produced from ANOVA analysis. Means and LSD's for % WSC utilisation presented are back-transformed from values produced by ANOVA analysis on arcsine transformed data.

		MGW		% WSC utilisation	
Variety	**Treatment**	**2016**	**2017**	**2016**	**2017**
Tower	**Control**	46.04	49.31	81.3	86.2
Tower	**Shade**	41.15	43.70	92.5	94.9
Volume	**Control**	34.24	39.72	93.0	93.0
Volume	**Shade**	31.54	35.07	92.2	96.9
Variety mean	**Tower**	43.6	46.5	86.9	90.5
	Volume	32.9	37.4	92.6	94.9
Manipulation mean	**Control**	40.1	44.5	87.2	89.6
	Shade	36.3	39.4	92.4	95.9

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	<0.001	2.59	<0.001	0.97	0.11	ns	0.001	0.03
Treatment (T)	**1**	0.011	2.57	0.002	2.46	0.009	0.03	<0.001	0.02
V*T	**1**	0.338	ns	0.655	ns	0.004	0.03	0.152	ns

The residual d.f were 3, and 6 for the main plot and sub-plot respectively

3.4 Discussion

The aim of this study was to determine the source-sink balance of both a two and a six-row variety during grain filling, along with investigating the impact of fungicide treatment and disease control on the source-sink balance in both row-types. It was hypothesised, following the observation of a similar response to fungicide treatment in chapter 2, that the source-sink balance would not differ between row-types. This was confirmed, through both source-sink manipulation experiments and the estimation of the amount of assimilate available for grain filling. Interestingly disease did not alter the source-sink balance in either variety.

In spite of the dramatically larger number of grains m^{-2} produced by the six-row variety Volume compared to the two-row Tower, the yield of fungicide treated crops appeared to be sink-limited in both row-types, and the relative source-sink balance was similar. The analysis is based on that presented by Bingham et al. (2007). These authors observed a decline in RUE of UK grown two-row winter barley during the post-anthesis period at some sites and in some seasons and provided evidence to suggest that this might be the result of feedback inhibition of photosynthesis from a low sink demand during grain filling. Similar evidence was presented in spring barley crops grown in Ireland (Kennedy, 2015). The potential yield was, therefore, estimated as the product of PAR interception by healthy tissue and the maximum RUE prior to any feedback inhibition, plus the amount of WSC in stems at the start of grain filling. The analysis assumes that all the WSC is potentially available for grain filling and no respiratory losses or partitioning to alternative sinks (e.g. roots) occurs. No account is made of dry matter, including protein, remobilised and transferred to the grain from leaves, roots and other tissues such as the rachis and awns. The reliability of the analysis depends on the accuracy of the estimates of HAint, RUE and WSC and the validity of the underlying assumptions. Thus some caution is required when interpreting the results.

Results suggest that source exceeded sink capacity in 2017 by an appreciable margin, but that in 2016 the source and sink were in closer balance. The 95% confidence limits in 2016 lay either side of zero suggesting that the true population mean was close to zero for this year. A potential yield less than the measured yield is theoretically impossible and suggests some error in estimating the source of assimilate for grain filling. There may have been some additional sources of dry matter for grain filling unaccounted for such as dry matter in roots and leaf laminae, or a possible upregulation of RUE late in grain filling. When biomass

accumulation was plotted against the interception of PAR by healthy tissue the relationship displayed a slight upward curve during grain filling in 2016 in all treatments, suggesting that there was a slight upregulation of RUE during grain filling. Interestingly measured yield was similar in both years, this is despite incident radiation being greater in the months of June and July in 2017 compared to 2016. These observations support the view that yield was more strongly sink limited in 2017 than 2016.

The findings of this study and other previous research (Bingham et al., 2007a, Serrago et al., 2013, Kennedy, 2015) indicate that the formation of sink capacity plays a vital role in yield formation in both two and six-row barley. They also demonstrate that the extent of sink limitation can vary widely with site and season (Bingham et al., 2007a; Bingham et al., 2019). Shading has been used to estimate the critical period for protection of canopy light interception required for grain filling in spring barley (Bingham et al., 2019). It was shown that yield was insensitive to shading during the latter part of grain filling, but that the duration of this period varied between crops reflecting likely variation in their source-sink balance. Evidence has also been presented of the upregulation of photosynthesis in barley ears when the canopy below the ears has been shaded (Serrago et al., 2013) indicating that the crop can adjust to changes in the source-sink balance during grain filling. In the present study retention of green leaf at GS55 plus four weeks was higher in 2017 compared to 2016 (data not presented) with percentage green area across the top three leaf layers being 41-45% when treated with fungicide in 2017, while values ranged from 7-9% for the same treatments in 2016. Thus it is possible that RUE was upregulated in 2016 due to the smaller green area to ensure maximum grain fill was achieved.

Although there was little difference in the source-sink balance between the two varieties in either year, there were small differences in the source of potentially available assimilate for grain filling. Thus Volume had a larger post-anthesis HAint and similar RUE to Tower, but a smaller stem WSC reserve at anthesis. The latter was the result of a smaller stem biomass m^{-2} rather than tissue concentration of WSC.

Results from the treatments to manipulate the source:sink ratio support the conclusion that grain filling of fungicide treated crops was sink limited and that Volume and Tower had a comparable source-sink balance. Although these experiments are not subject to the range of

possible measurement errors associated with estimating potential yield, they do introduce a different set of uncertainties that will be discussed below.

Where assimilate supply was increased per grain (de-graining and row-opening) MGW was increased. The manipulation methods varied in the scale of their adjustment to the source:sink ratio, with de-graining increasing potential assimilate supply per grain by 100%, and row-opening by 10-24%. As the effects of row opening on light interception were only measured on one replicate of each variety and in 2017 only, caution should be taken when interpreting the crop's response to the scale of the change. However, it can be said that the scale of adjustment of the source:sink ratio was smaller with row-opening compared to de-graining. Despite this variance, the increase in MGW was similar in both treatments. Where the source availability per grain was reduced (shading) MGW reduced accompanied with an increase in the amount of WSC utilised during grain filling.

Importantly the changes in MGW caused by manipulating the source:sink ratio did not match the relative change in assimilate supply. Borrás et al. (2004), in a review of the seed dry weight response caused by source-sink manipulations concluded that the adjustment in MGW should be of similar magnitude to the change in assimilate supply in order to qualify as source limitation. Adjustments in grain weight that are substantially less, or where no adjustment at all is observed, may be interpreted as evidence of co- or sink-limitation. Treatments that both increase and decrease the source:sink ratio are required for a more complete understanding. For example de-graining and row opening of fungicide treated crops increased MGW by around 8% in response to an increase in assimilate supply per grain of up to 100% (with de-graining). Taken on their own these results might suggest that grain filling in non-manipulated crops was source limited, thus an increase in assimilate supply increased grain weight until the source exceeded the sink capacity. However, if grain filling was source limited, a near one to one reduction in grain weight would be expected when assimilate supply was reduced by shading. In fact a 74% reduction in incident light with shading reduced MGW by only 10 to 11%. An increase in utilisation of stem WSC reserves plus possible compensatory increases in RUE under shades (Kennedy, 2015) may have buffered grain filling against the decrease in incident light. However, these effects are unlikely to account for the small magnitude of response of grain weight to shading. Thus, the manipulation treatments suggest that grain filling was co-limited by source and sink with the major control being via sink capacity (Boras et al., 2004). Moreover, the response to

these manipulations of the source:sink ratio was similar in both varieties, although the MGW of Volume in the absence of a source limitation (i.e. after de-graining) never reached the value of Tower. This would indicate that the six-row Volume has a lower PGW compared to the two-row Tower.

Crops that were not treated with fungicide developed more disease and intercepted less PAR by healthy tissue than crops which were treated with fungicide. This effect was also associated with a reduction in RUE, although to a lesser extent in Volume compared to Tower. Some studies have linked the effects of foliar pathogens on RUE to the nutritional type of the pathogen. Evidence has been presented which shows that leaf rust (*P. triticina*) (biotroph) in wheat had a larger effect on RUE compared to tan spot (*Pyrenophora tritici-repentis*) (necrotroph) due to a reduction in leaf nitrogen and increased assimilate consumption in leaf respiration (Schierenbeck et al., 2016). The disease spectrum did not vary drastically between the years and varieties. Tower had a higher level of infection of the spot form of net blotch in 2017 compared to Volume and Volume a higher level of powdery mildew (biotroph), but the total amount of disease did not differ between varieties at any stage during the season. If the finding by Schierenbeck et al (2016), was to occur in this study then it would be expected that the RUE of untreated Volume should be lower than Tower reflecting the higher level of mildew infection in Volume. Volume being an F1 hybrid may benefit from hybrid vigour although there is no evidence to suggest this involves a greater RUE. No study has investigated the effect of hybrid varieties on RUE over inbred lines in barley, although studies have been carried out on rice concluding that the RUE of hybrid and inbred varieties does not differ (Katsura et al., 2008, Zhang et al., 2009).

There was no evidence that grain filling in untreated crops was source-limited even though healthy area light interception was reduced relative to those treated with fungicide. The difference between estimated potential yield and measured yield was the same as that in fungicide treated crops and indicative of sink limitation. Moreover, the response to manipulation of the source:sink ratio was the same as in treated crops. Thus de-graining increased MGW of untreated crops to the same extent as treated crops, as did row opening. There was no significant interaction between fungicide and manipulation treatments on MGW. Similarly there was no difference in the response of untreated Tower and Volume to changes in the source:sink ratio suggesting that in diseased crops, as in fungicide-treated crops, the source-sink balance of Volume was comparable to that of Tower. Thus, the larger

grain number of Volume did not appear to increase its risk of source-limitation in the absence of fungicide treatment. Therefore it must be questioned as to why untreated crops were not source limited. Although the source capacity of these crops was lower than those treated with fungicide, their sink capacity was in turn also lower.

Disease was controlled by fungicide treatment when assessed at GS39 in 2017 only and GS55 in both years. The control of disease during this period may have increased sink capacity as this period is critical for the formation of the number of grains m^{-2} (Arisnabarreta and Miralles, 2008a) and it has been suggested that PGW may also be determined during this period (Scott et al., 1983, Kennedy, 2015). However, disease levels in the top three layers of the canopy at GS39 and GS55 in both years were low, with mildew and Septoria nodorum dominating, although there was a higher level of disease lower down in the canopy (layers 4 and 5) in untreated crops (data not presented). The effects of this disease on PAR interception by healthy tissue was statistically significant in 2016, but the difference between fungicide treated and untreated crops was small (4.8 MJ m^{-2} PAR) for the period of GS31-55. In 2017 the effect was not significant with the difference in PAR interception being less than 1 MJ m^{-2} PAR. It must be questioned whether these small changes in PAR interception by healthy tissue would have any impact on the development of grain sink capacity.

In both years there was a significant increase in the number of grains m^{-2} when comparing fungicide treated and untreated programmes. Fungicide treatment also increased PGW relative to untreated crops as observed in the MGW after de-graining; this effect was similar in both years (+12% in 2016 and +18% in 2017). Direct physiological effects of fungicides could have contributed to the observed increase in sink capacity as evidence of direct effects on sink capacity has been published previously (Bingham et al., 2014, Bingham et al., 2012).

The six-row variety Volume and two-row variety Tower, responded similarly to fungicide. Despite dramatically different yield components, altering the source:sink ratio during grain filling led to a similar MGW response in both varieties, indicating a similar source-sink balance. Moreover, there was no difference the response of MGW caused by source-sink manipulations between fungicide treated and untreated crops. This result is consistent and provides reason behind the result presented in chapter 2 showing that the response to fungicide programmes did not differ between both row-types.

3.5 Conclusion

Despite the larger number of grains m^{-2} produced by the six-row variety the source-sink balance of this variety during grain filling was comparable of that of the two-row variety. Yield in both row-types was largely sink-limited, while fungicide treatment did not impact on the source-sink balance. This was because the increase in source arising from fungicide treatment was accompanied by a corresponding increase in sink capacity.

Chapter 4 **Sensitivity of grain sink capacity to variations in pre-anthesis photosynthetically active radiation in a conventional two-row and hybrid six-row barley variety**

4.1 Introduction

The world's population consumes the majority of their daily calorie intake from the carbohydrates stored in cereal grains. Thus, identifying routes to increase yield through plant breeding and understanding the implications this may have for crop management have become critical research goals for all the major cereals. Although the major uses of barley globally are for animal feed and malt production, there has been renewed interest in using barley for human food. This has been mainly in the developed world where there is a drive towards including more whole grains in diets for health benefits (Ullrich, 2010). Barley grains contain ß-glucans, which have been found to be effective in lowering blood cholesterol (Pins and Kaur, 2006). However, improvements in yield cannot be made at the expense of grain quality. For all the major end uses of barley, high quality, large grain is important. For example, large grain size is related to the low protein and high starch content (Yu et al., 2017) required by the malting industry, while larger grain has also been shown to contain more ß-glucans (Elfverson et al., 1999). Thus, yield increases must be sought whilst maintaining an acceptable average grain weight.

Grain weight is determined by 1) the capacity of the grain for starch storage (referred to here as potential grain weight (PGW)), or 2) the supply of assimilate per unit grain number for grain filling (Evans and Wardlaw, 2017). It can therefore, be limited by both source and sink. Experiments conducted in Chapter 3 demonstrated that mean grain weight (MGW) in both a two- and six-row variety was more sink- than source-limited. Large variations in post-anthesis assimilate supply per grain induced by shading, de-graining and row opening treatments (100% in the extreme case) translated into only small changes (~10%) in grain weight. In fact, the lower MGW in the six-row variety, Volume was due to a lower PGW compared to the two-row, Tower and not differences in their source-sink balance, as this was comparable in spite of the large disparity in grain number m^{-2}.

Presently there is a poor understanding of the mechanisms controlling PGW and the developmental phases over which they operate. A growing body of evidence points towards PGW being under maternal control and that effects may operate either pre- or post-anthesis (Brinton and Uauy, 2018). Several studies have related final grain weight at harvest to the weight of the carpels at anthesis in wheat (Guo et al., 2016, Xie et al., 2015, Hasan et al., 2011), sunflower (Castillo et al., 2017) and barley (Scott et al., 1983). Endosperm cell number has also been correlated with final grain weight in barley (Cochrane and Duffus, 1983). It has been suggested that PGW may be limited by the husk (outer seed layer) placing a physical restriction on the storage volume (capacity) of the grain (Habgood and Uddin, 1983, Scott et al., 1983). In more recent times the important role of the seed coat (pericarp; maternal tissue) in early grain development has been reported. Genes that are suspected of controlling endosperm cell number have been shown to be strongly transcribed in the pericarp whilst weakly transcribed in the endosperm (Izawa et al., 2009). Programmed cell death in the pericarp has been shown to be an important influence on grain size. Timely PCD of the pericarp provides assimilate and space for endosperm cell formation and expansion during early grain development, while delayed PCD was shown to reduce the storage capacity of the grains (Volodymyr et al., 2018).

Grain number is sensitive to variations in assimilate availability during ear development (Arisnabarreta and Miralles, 2008a, Benincasa et al., 2017, Acreche et al., 2009). An increase in grain number, may result in a reduction in grain weight, as shown by (Acreche et al., 2009). Such corresponding adjustments in grain weight have generally be interpreted in terms of changes in the amount of assimilate available per unit grain number for grain filling. However, the synchronous determination of grain number and PGW during ear development would provide an alternative mechanistic explanation for the reported trade-off between grain number and grain weight (Quintero et al., 2018). At present, however, the effects of pre-anthesis growth conditions on PGW are not well documented.

The possible implications of an early determination of PGW for crop management, including disease management, are clear. Not only is the period between stem extension and anthesis a critical period for ensuring grain number formation is maximised, it could also be critical for the determination of final grain weight and thus grain quality for the end uses outlined above. While, six-row varieties produce a larger number of grains ear^{-1}, their higher rate of spikelet mortality compared to two-row varieties (Arisnabarreta and Miralles, 2006)

suggests there may be a greater demand for resources during this period in a six-row variety. Thus, it is conceivable that the relationship between grain number formation and PGW is more sensitive to variations in assimilate availability to the ear during carpel development in a six-row compared with a two-row variety.

Experiments presented here had three objectives. Firstly, to determine the relative effects of varying light availability to the crop during late stem extension on ear growth and carpel weight at anthesis of a two-row and six-row variety of barley. Secondly, to determine whether the effects of pre-anthesis conditions on ear growth and carpel weight influenced PGW. In wheat, carpels in florets furthest from the rachis were found to be lighter than those closer to the rachis (Xie et al., 2015, Hasan et al., 2011, Guo et al., 2016), with these differences correlating with differences in final grain weight at these floret locations. It is possible, therefore that carpels and grains in central spikelets of six-row barley respond differently to variations in assimilate availability during ear development than those in lateral spikelets. A third objective, therefore, was to assess the effects of treatments to vary assimilate availability on grain growth in central and lateral spikelet positions and its impact on the MGW in a six-row variety.

The following hypotheses were tested:

1. Increasing light availability during stem extension will increase ear growth rate and carpel weight at anthesis, while decreasing light availability during the same period will decrease ear growth rate and carpel weight at anthesis.
2. These changes in ear growth rate and carpel weight will translate into effects on final grain weight.
3. Due to the higher number of grains ear^{-1} the sink capacity in a six-row variety will be more sensitive to variation in light availability during stem extension.
4. Carpels and grains in the lateral spikelet positions in a six-row ear will be more sensitive to changes in light availability compared to those in the central positions.

4.2 Materials and methods

4.2.1 Site and general husbandry

Field experiments were conducted in 2016/17 (hereafter called 2017) and 2017/18 (2018) growing seasons at Teagasc, Oak Park, Carlow, Ireland. The soil type was a loam with moderate moisture-holding capacity. In each season the previous crop was winter wheat. Plots were established following inversion ploughing and harrowing, seed treated with Redigo Deter ® (50 g l^{-1} prothioconazole and 250 g l^{-1} clothianidin, Bayer Crop Science, Monhem am Rhein, Germany) was drilled on the 30th September 2016 and 1st October 2017 with a Wintersteiger Plotseed XL drill (Wintersteiger AG, Austria) at a seed rate of 360 viable seeds m^{-2}. Plot size was 2.5 x 12m. A total of 190 kg N ha^{-1} was applied in two applications in the form of calcium ammonium nitrate, one-third of the total at mid to late tillering (GS25-29) and two-thirds at the onset of stem extension (GS30). Other nutrients (P, K and S) were applied at rates not to limit crop growth and development, in accordance with the regulations (Wall and Plunkett, 2016). Herbicides were applied to limit the impact of weeds on crop growth, fungicides were applied at GS25-29, GS31/32 and GS49 to limit the impact of foliar diseases. Plant growth regulators were applied to prevent lodging. Seasonal meteorological data were obtained from an onsite weather station <2km from the experiment. Full husbandry details can be found in Appendix 2

4.2.2 Treatments and Experimental Design

The experimental design was a split-split plot with three factors (variety, pre-anthesis manipulation, post-anthesis de-graining) randomised in four replicate blocks.

Two varieties were randomised within main plots, an F1 hybrid six-row, Volume (Syngenta, Basel, Switzerland) and a conventional two-row variety, KWS Tower (KWS UK Ltd, Thriplow, UK). Pre-anthesis assimilate supply treatments were randomised in sub-plots. Here, two manipulation methods were used; shading and row-opening as described below. Controls were equivalent randomised areas marked out within each sub-plot, but with no treatment imposed. A de-graining treatment was applied to main shoot ears within sub-sub-plots; intact ears served as controls.

Pre-anthesis manipulations

Shading was used to decrease assimilate supply by reducing the amount of light the crop intercepted. The shading material used was an open weave black polystyrene shade-netting (Tildenet Ltd., Bristol, UK). Shades were 2 x 3m in size and were erected 0.5m above the crop canopy using the system described by (Kennedy et al., 2018) and in Chapter 3. The shades were erected on wooden fencing posts and a rope frame shown in Figure 4-2. A pyranometer (SPLite2, Kipp & Zonen B. V., Delft, Netherlands) and a relative humidity/temperature probe (MP100A, Rotronic Instruments (UK) Ltd., Crawley, UK) connected to a data logger (CR1000, Campbell Scientific Ltd., Loughborough, UK) were used to measure climatic conditions in shaded and un-shaded areas for a total of 8 days in 2017 and 8 days in 2018 (Figures 1.3 &1.4). Assessments of lodging (>45° from vertical), leaning (5-45° from vertical) and brackling (stem failure >1/3 up from the base) in treated and untreated areas were conducted after the treatments were removed.

Row-opening was used to increase assimilate supply by increasing light availability to the designated plant row. Adjacent rows along a 3m long row were pushed back using a system of white fencing stakes and bailing twine shown in Figure 4-1. Rows were monitored regularly to ensure that the adjacent rows had not closed in. The increase in light inception by the exposed row caused by row-opening was measured using a SunScan Canopy Analysis System at GS55 (Delta-T devices, Cambridge, UK). The lance of the device was placed along an unopened row of plants, the incident PAR and PAR transmitted to the base of the canopy was simultaneously measured five times. Plants were removed along the length of the lance, incident and transmitted PAR was re-measured five times again. The number of shoots removed was recorded. This procedure was repeated for a row that was opened and for each variety. These were replicated measurements made on a single plot each of variety Tower and Volume. It must be noted that this was done at GS55 and was the same set of measurement carried out in chapter 3. During the pre-anthesis period there will be less competition from adjacent rows, thus the increase in light could be less than values indicate

The de-graining treatment was to ensure that potential grain weight was reached as results in Chapter 3 showed a significant increase in grain weight from post-anthesis de-graining. De-graining was carried out on 10 tagged main shoot ears in each sub-plot using the same

methods as described in Chapter 3. The top half of the ear was removed two weeks after anthesis without damaging the awns of the remaining grains.

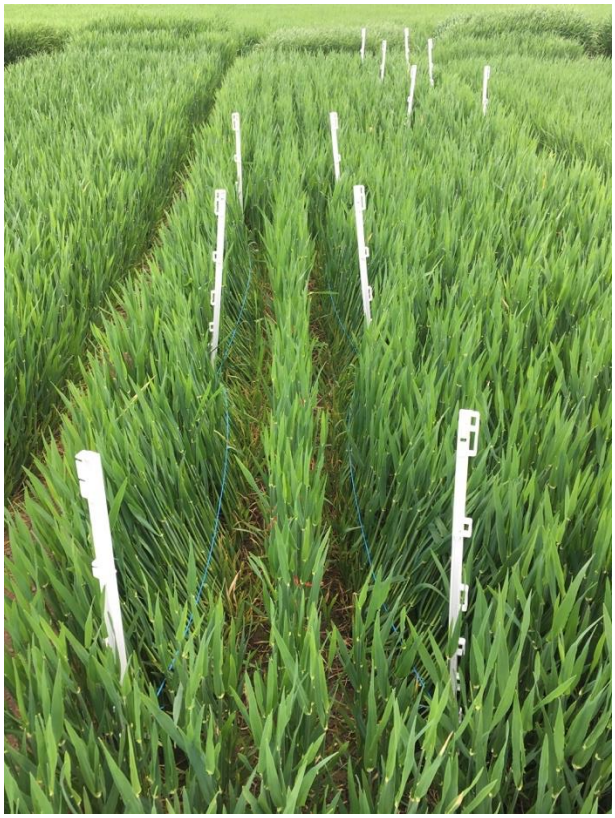

Figure 4-1. Row-opened plot

Figure 4-2 Shaded plot

Figure 4-3 Relative humidity, temperature and solar radiation senor under the shade

Figure 4-4 Relative humidity, temperature and solar radiation senor outside the shade.

4.2.3 Treatment period and date of fertilization and anthesis

Shading and row opening treatments were imposed approximately three weeks prior to fertilization and anthesis on the 21st April 2017 and 26th April 2018. The imposition of treatment corresponded with the date of final (flag) leaf emergence (GS39) on the main shoots.

In order to identify precisely when fertilization had occurred, the method and the developmental scale of Waddington et al. (1983), was used. As booting and ear emergence progressed, five main shoots were sampled each day, and the spikelets on the central part of the ear dissected open to reveal the carpel. Fertilization was deemed to have occurred when pollen was visible on the stigma on 50% of the assessed shoots. Fertilization occurred on the 10th May 2017 and 16th May 2018, corresponding with GS55. Anthesis (extrusion of the anthers) was observed on some ears at GS55. For the purposes of this study we have taken fertilization, 50% ear emergence and anthesis to occur at the same time.

Pre-anthesis shoot growth

All plant measurements were carried out on tagged main shoots. Main shoots were tagged at GS31 using a non-destructive black netting and twine. Within each sub-plot, main stems in both control and manipulation areas were tagged.

Every 3-5 days during the pre-anthesis treatment period five randomly selected tagged main shoots from treatment and control sub-plots were cut at ground level. Shoots from a given sub-plot were placed into a polyethene bag within a cool box (4-6°C). Sampling was carried out between the hours of 10:00-12:00. Samples were then transported to the lab and processed immediately. Processing was carried out one sample at a time. Any dirt was first removed from the base of the shoots; following this shoots were separated into leaves and stem, then the ear was dissected out of each stem. Each fraction was weighed fresh with leaves and stems being weighed to the nearest 0.01g while developing ears were weighed to the nearest 1mg. Fractions were then immediately placed in a fan-assisted oven at 110°C for 2 hours to rapidly kill the tissue after which the temperature was reduced to 70°C and the tissue dried for 48 hours or to a constant mass. Once dry, the weight of each fraction was recorded again to the nearest 0.01g for leaves and stems and 1mg for ears.

Carpel weight at anthesis

Once fertilization was observed to have occurred an additional five randomly selected tagged main shoots from each treatment and control sub-plot were cut at ground level, pooled together, and brought to the lab for processing. If processing was delayed, samples were stored for no more than two days in a cold room (4-6°C) until processing took place. Samples were separated into ear, leaf and stem fractions. Leaves and stems were placed in an oven at 70°C for 48 hours. To determine the carpel weight, the number of spikelets on one side of the ear was counted, divided by two and rounded up to the nearest whole number; this identified the middle spikelet position. In the two-row variety, the central spikelets at this middle location were then carefully removed on both sides of the ear along with the spikelet positions immediately above and below them. For the six-row variety, central and lateral spikelets were identified, with lateral spikelets on both sides of each central spikelet also being removed for separate analysis. In total there were six spikelets removed per ear for the two-row variety while 18 were removed (six central and twelve lateral) in the six-row variety. All carpels from each sample were then dissected from the spikelets, weighed fresh to the nearest 1mg and dried at 70°C for 48 hours. Dry weight was then determined to the nearest 1mg.

Harvest measurements

Once the crop had reached physiological maturity (GS87) ten main shoots and ten de-grained ears from each treatment area were sampled. Shoots were again cut at ground level, those from a given sub-plot and de-graining treatment pooled together and brought to the lab for processing. Samples were placed in a sealed glasshouse on raised racks for 2-3 days to air dry before processing. Samples were divided into ears, leaves and stems then oven dried at 70°C for 48 hours. When dry the weight of each fraction was recorded to the nearest 0.01g. Non-de-grained (control) ears were then divided into two sub-samples of 5 ears each. Ears in the first were divided into top and bottom halves, hand threshed between two pieces of foam board, the grain was cleaned using a winnower to remove awns and chaff, weighed, all grains counted using an automated grain counter (Pfeuffer GmbH, Kitzingen, Germany) and mean grain weight determined to the nearest 1mg. The second sub-sample was used for comparison of final grain weight with carpel weight at anthesis for the same middle spikelet locations on the ear. The same procedure used for the determination of carpel weight was

followed on each ear with individual grain weight in the middle positions of the ear determined to the nearest 1mg.

4.2.4 Statistical analysis and calculations

The effects of pre-anthesis shading and row-opening treatments were analysed separately as manipulations were not contained in the same plot. All statistical analyses were carried out using GenStat (18th Edition, VSN International Ltd., Hemel Hempstead, UK)

To calculate the effect of shading on incident solar radiation, data recorded in kWh m^{-2} were converted MJ m^{-2} per day. PAR was then estimated as 0.5 x solar radiation (McCree, 1981). Climatic conditions under and outside the shaded area were recorded every hour. Daily average temperature, relative humidity (RH) and incident PAR was calculated for the period during treatment both 2017 and 2018. The effect of shading on the climatic conditions was then analysed using a two-way ANOVA with day as the unit of replication.

The increase in light interception caused by row-opening was calculated as described in Chapter 3, again indicating a 45% and 10% increase in the amount if light intercepted per row in Tower and Volume receptively

The growth rate of each fraction was calculated using equation 8.

$$\frac{(W_f - W_i)}{(T_f - T_i)} \qquad 8)$$

Where W_i is the weight of the fraction at the imposition of treatment, W_f is the weight of the fraction at anthesis, T_i is the date of imposition of treatment and T_f is the date of anthesis. Growth rate was then calculated for the sum of 5 shoots per replicate each.

The proportion of total biomass partitioned to each of the fractions (ear, leaf and stem) at anthesis was calculated using equation 9

$$\frac{Fraction\ biomass}{Total\ biomass} \qquad 9)$$

Where fraction biomass was the biomass of each individual fraction at anthesis (average of 5 shoots per sample) and total biomass was the total biomass of the sample at anthesis.

The effects of pre-anthesis manipulations on growth rate, carpel weight, biomass proportion for each fraction, grains ear^{-1} was analysed using a split-plot ANOVA model where effects of variety and pre-anthesis manipulation were analysed within the fixed model for each year individually, while replicate was included in the blocking structure. The lateral spikelet positions were removed from the analysis.

The effect of pre-anthesis manipulation and post-anthesis de-graining on MGW from the bottom half of the ear was analysed using a split-split plot ANOVA model where effects of variety, pre-anthesis manipulation and post-anthesis de-graining was analysed in the fixed model for each year individually. Replicate and year were included in the blocking structure.

The effects of spikelet/grain position (central or lateral) on carpel weight and final grain weight from the middle portion of the ear at harvest was analysed with data from the two-row variety removed, using a split-plot ANOVA model - where effects of pre-anthesis manipulations and spikelet/grain position were analysed in the fixed model for each year individually. Year and replicate were included in the blocking structure.

Normality was checked using a probability of distribution test in GenStat (18th Edition, VSN International Ltd., Hemel Hempstead, UK), while homogeneity was checked using Bartlett's test.

Further correlation and regression analysis

Simple linear regression was carried out to investigate the influence of carpel weight at anthesis, ear dry weight at anthesis and ear growth rate during the pre-anthesis treatment period on the final weight of grains from central spikelet positions at the mid-section of the ear. For the purpose of this analysis data were separated into groups based on variety and year with values pooled over manipulation treatments.

4.3 Results

4.3.1 Meteorological data

The growing season for each experiment is defined as October to July. Long term (1981-2010) total rainfall was 699mm for the growing season, while the long-term average temperature during the same period was 8.9°C. Cumulative global radiation had a seasonal average of 2698 MJ m^{-2} in the period from 2008-2014. Both experimental seasons were

warmer and drier than normal, with the average temperature for each being 9.3°C and accumulated rainfall values of 528 mm and 591 mm for 2017 and 2018 respectively. It must be noted that a drought occurred during the months of May and June in 2018, soil moisture deficits were reported as high as 80 mm using methods described by (Schulte et al., 2005) and partial drought was recorded for 52 days in Oak Park from the 28th May until the 19th July. With partial drought being defined as a period of at least 29 consecutive days where the mean daily rainfall does not exceed 0.2 mm (Anon., 2018d). Between the 13th May and 22nd July 2018 there was a total of only 13.7 mm of rain. There was a greater accumulated solar radiation than normal in each season with values of 2826 MJ m^{-2} and 2974 MJ m^{-2} in 2017 and 2018 respectively.

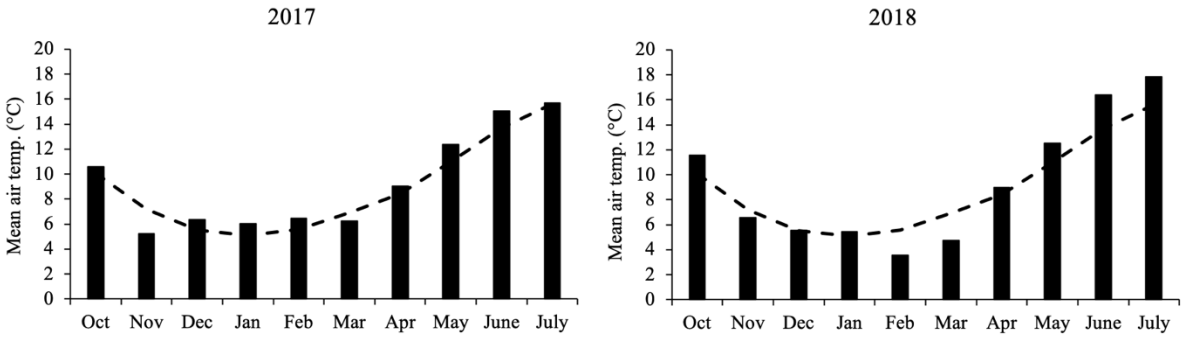

Figure 4-5. Monthly mean temperature (°C) from October to July for 2017 and 2018 seasons. Broken line shows long term averages (1981-2010)

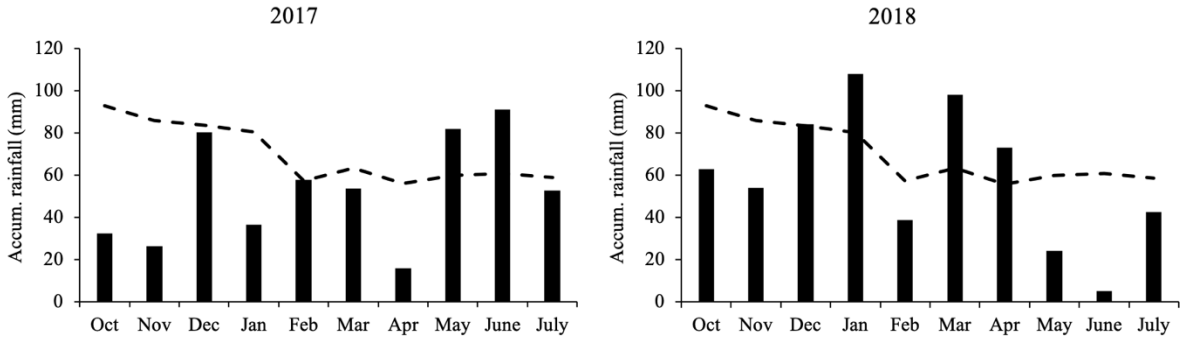

Figure 4-6. Monthly accumulated rainfall (mm) from October to July for 2017 and 2018 seasons. Broken line shows long term averages (1981-2010).

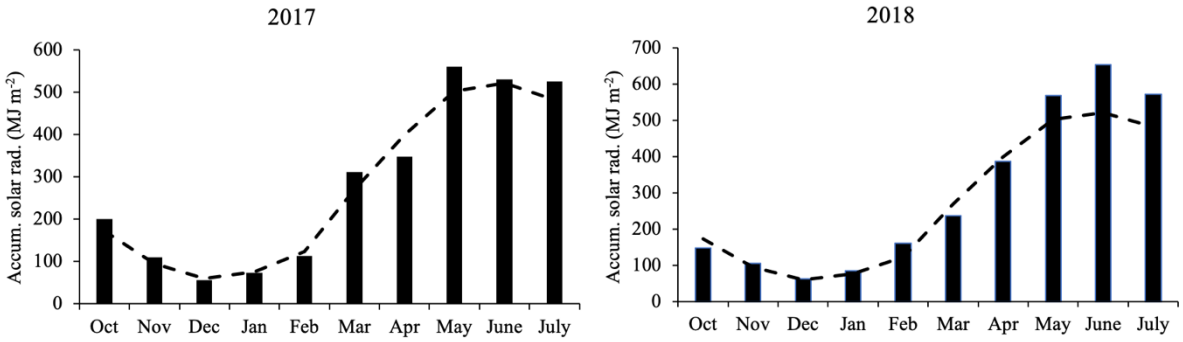

Figure 4-7. Monthly accumulated solar radiation (MJ m^{-2}) from October to July for 2017 and 2018 seasons. Broken lines shows long-term average (2008-2014).

4.3.2 Pre-anthesis manipulation effects

Row opening increased the amount of photosynthetically active radiation (PAR) intercepted per row by 45% in Tower and 10% in Volume. This measure was done at GS55 in one replicate of each variety in 2018 only so should be taken with caution.

The effect of shading on PAR, relative humidity and temperature is shown in Table 4-1. Shading significantly decreased the PAR incident on the crop by 64% in 2017, and 72% in 2018 ($p>0.05$), while relative humidity was significantly (~2%) in each year ($p>0.05$). The effect of shading on temperature was not significant in 2017 ($p<0.05$), while it was significant in 2018, increasing temperature by 0.5 ^{o}C.

Table 4-1 Effects of shading on the meteorological environment beneath the shade compared with unshaded conditions.

Year	Treatment	Average daily PAR MJ m^{-2}	Average daily RH %	Average daily Temp ^{o}C
2017	**Shaded**	2.19	67.2	10.7
	Unshaded	6.03	69.1	10.9
2018	**Shaded**	2.50	82.5	11.2
	Unshaded	8.80	88.4	10.7
effect of shading %	**2017**	-63.68	-2.82	Ns
	2018	-71.61	-6.73	4.69
Year	**df**	P-value	P-value	P-value
2017	7	<0.001	<0.001	0.152
2018	7	<0.001	<0.001	<0.001

4.3.3 Growth rate and biomass at anthesis of different shoot fractions

Total shoot growth rate and biomass

The interaction between variety and manipulation treatment was not significant for the total shoot growth rate during the three week period prior to anthesis for either row-opening or shading in both 2017 and 2018 ($p>0.05$) (Table 4-2 and Table 4-3). Pre-anthesis shading significantly decreased total growth rate by 42% and 32% in 2017 and 2018 respectively ($p<0.05$), while row-opening significantly increased total growth rate by 39% and 6% in 2017 and 2018 respectively ($p<0.05$). In shading treatments, Volume had a 83-74% higher total growth rate compared to Tower in both years ($p<0.05$), while in row-opening treatments the total growth rate was significantly higher (54%) in Volume in 2017 only.

The interaction between variety and both pre-anthesis treatments was not significant for the amount biomass per shoot at anthesis in 2017 or 2018 ($p>0.05$) (Table 4-4 and The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-5). Pre-anthesis shading significantly decreased total biomass at anthesis ($p<0.05$), while row-opening significantly increased total biomass per shoot at anthesis in 2017 but not 2018 ($p<0.05$). When averaged over the manipulation treatments, Volume had 46-48% more biomass per shoot compared to Tower in 2017 and 20-42% more in 2018 (depending on the manipulation treatment examined).

Ear growth rate and biomass at anthesis

Ear growth during the period of treatment is presented in Figure 4-8 and Figure 4-9. In 2017 growth was largely linear during the period of treatment with differences in ear weight being noticed towards to the end of the treatment. In 2018 the effects of treatments were visible earlier during the treatment period. For both shading and row-opening treatments in 2017 and 2018 the variety x manipulation interaction on ear growth rate was not significant ($p<0.05$). Shading significantly decreased ear growth rate in both 2017 (-24.2%) and 2018 (-24.5%) ($p<0.05$) and row-opening significantly increased ear growth rate in 2017 (+10.8%) ($p<0.05$) compared to controls, but not in 2018 (Table 4-2 and Table 4-3). Growth rate of the developing ear was significantly higher in Volume compared to Tower ($p<0.05$) in both pre-anthesis manipulations and both years.

The interaction between variety and manipulation was not significant for ear biomass at anthesis for all manipulation/year combinations ($p>0.05$) (Table 4-4 and The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-5). Shading reduced ear biomass at anthesis by 22-23% ($p<0.05$). Although row-opening did not cause any statistically significant change in ear biomass at anthesis, there was a small (7%) increase in 2017 ($p=0.069$) when averaged over varieties.. For all manipulation/year combinations Volume had between 53-87% more biomass in the ear at anthesis compared to Tower depending on year and manipulation ($p<0.05$).

The proportion of biomass partitioned to the developing ear was not significantly affected by the interaction between variety and row-opening in either year ($p>0.05$) (Table 4-6). By contrast, shading in 2018 caused a reduction in the amount of biomass partitioned to the developing ear in Tower, but not Volume (Table 4-7). This difference in response led to a significant ($p<0.05$) interaction between variety and shading on ear biomass ratio in 2018. Averaged across varieties, relative biomass partitioning to the ear was unaffected by row opening in 2017 and 2018, or shading in 2017. Volume had a higher proportion of biomass partitioned to the ear at anthesis compared to Tower ($p<0.05$) in all manipulation/year combinations except shading in 2017.

Leaf growth rate and partitioning

Over the treatment period leaf biomass declined (Table 4-2 and Table 4-3). The row-opening x variety interaction was not significant in 2017 ($p>0.05$), however, it was in 2018 ($p<0.05$). In 2018 the reduction in biomass was greater in the control treatment compared to row-opening in Tower, whereas in Volume the opposite was true. The variety x shading interaction was not significant ($p>0.05$) in either years. There was no significant main effect of variety or manipulation in either year ($p>0.05$).

When investigating the effects of manipulation on the proportion of biomass partitioned to the leaf, the interaction between variety and manipulation was not significant in either year or type of manipulation treatment ($p>0.05$). Shading significantly increased by 13-17% the proportion of biomass partitioned to the leaf at anthesis ($p<0.05$) (Table 4-7), but row-

opening had no significant effect ($p>0.05$) (Table 4-6). There was no significant overall difference between varieties in either type of manipulation or year ($p>0.05$).

Stem growth rate and partitioning

The interaction between variety and manipulation on stem growth rate was not significant for row-opening or shading in either year ($p>0.05$) (Table 4-2 and Table 4-3). Pre-anthesis shading significantly decreased stem growth rate by 45% and 36% in 2017 and 2018 respectively ($p<0.05$) (Table 4-3), while row-opening significantly increased stem growth rate by 45% in 2017 only ($p<0.05$) (Table 4-2). Volume had a higher overall stem growth rate than Tower when crops were shaded (61-65%) in both years and row-opened in 2017 (35%) ($p<0.05$).

For all manipulation/year combinations the interaction between variety and manipulation was not significant for the amount of biomass partitioned to the stem ($p>0.05$). Row-opening did not significantly affect the proportion of biomass partitioned to the stem in either year ($p<0.05$) (Table 4-6), while shading decreased it ($p<0.05$), but only in 2018 and by as little as 2% (Table 4-7). In all manipulation/year combinations Tower partitioned significantly more biomass to the stem compared to Volume ($p<0.05$).

Table 4-2. Effects of pre-anthesis row-opening (RO) on the growth rate (g day^{-1}) of ear, leaf, stem and total (whole) shoots. Means, p values and LSD's were produced from ANOVA anaylsis.

		Row-opening							
Variety	**Treatment**	**Ear**		**Leaf**		**Stem**		**Total**	
		2017	**2018**	**2017**	**2018**	**2017**	**2018**	**2017**	**2018**
Tower	**Control**	0.064	0.053	-0.012	-0.006	0.113	0.127	0.164	0.174
Tower	**RO**	0.074	0.058	-0.006	-0.001	0.161	0.125	0.229	0.182
Volume	**Control**	0.119	0.081	-0.016	-0.003	0.151	0.116	0.253	0.194
Volume	**RO**	0.128	0.090	0.003	-0.013	0.221	0.133	0.353	0.210
Variety Mean	**Tower**	0.069	0.056	-0.009	-0.004	0.137	0.126	0.197	0.178
	Volume	0.123	0.085	-0.007	-0.008	0.186	0.125	0.303	0.202
Treatment mean	**Control**	0.091	0.067	-0.014	-0.005	0.132	0.122	0.209	0.184
	RO	0.101	0.074	-0.001	-0.007	0.191	0.129	0.291	0.196

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.001	0.014	0.002	0.010	0.553	ns	0.080	ns	0.046	ns	0.941	ns	0.014	0.065	0.353	ns
Treatment (T)	**1**	0.025	0.008	0.232	ns	0.083	ns	0.474	ns	0.002	0.028	0.534	ns	0.005	0.047	0.447	ns
V*T	**1**	0.946	ns	0.710	ns	0.352	ns	0.044	0.007	0.358	ns	0.443	ns	0.400	ns	0.792	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-3. Effects of pre-anthesis shading on the growth rate (g day^{-1}) of ear, leaf, stem and total (whole) shoots. Means, p values and LSD's were produced from ANOVA anaylsis.

		Shading							
		Ear		Leaf		Stem		Total	
Variety	**Treatment**	**2017**	**2018**	**2017**	**2018**	**2017**	**2018**	**2017**	**2018**
Tower	**Control**	0.062	0.049	-0.010	-0.009	0.115	0.082	0.166	0.122
Tower	**Shaded**	0.049	0.035	-0.007	-0.005	0.076	0.054	0.106	0.084
Volume	**Control**	0.123	0.082	-0.004	-0.004	0.206	0.137	0.324	0.215
Volume	**Shaded**	0.091	0.064	-0.018	-0.007	0.102	0.087	0.175	0.144
Variety mean	**Tower**	0.055	0.042	-0.009	-0.007	0.095	0.068	0.136	0.103
	Volume	0.107	0.073	-0.011	-0.005	0.154	0.112	0.250	0.180
Treatment mean	**Control**	0.092	0.066	-0.007	-0.007	0.160	0.109	0.245	0.169
	Shaded	0.070	0.050	-0.013	-0.006	0.089	0.070	0.141	0.114

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.002	0.017	<0.001	0.007	0.670	ns	0.717	ns	0.021	0.042	0.019	0.031	0.022	0.083	0.015	0.048
Treatment (T)	**1**	0.008	0.014	<0.001	0.005	0.186	ns	0.824	ns	0.005	0.040	<0.001	0.014	0.007	0.065	<0.001	0.017
V*T	**1**	0.145	ns	0.424	ns	0.051	0.015	0.214	ns	0.098	ns	0.095	ns	0.140	ns	0.053	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

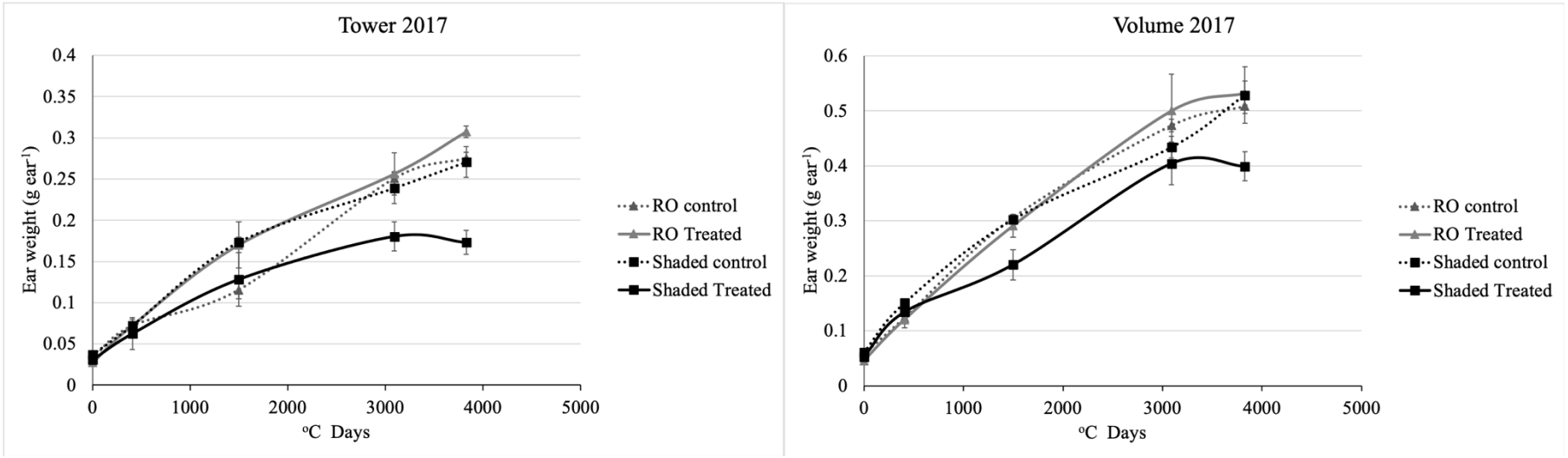

Figure 4-8. Ear weight per shoot plotted against thermal time (ºC days) during the treatment period in 2017. Error bars represent standard error of the mean. Dotted lines represent controls while solid lines represent treated. Triangles represent row-opening (RO) treatments, while squares represent shading treatments.

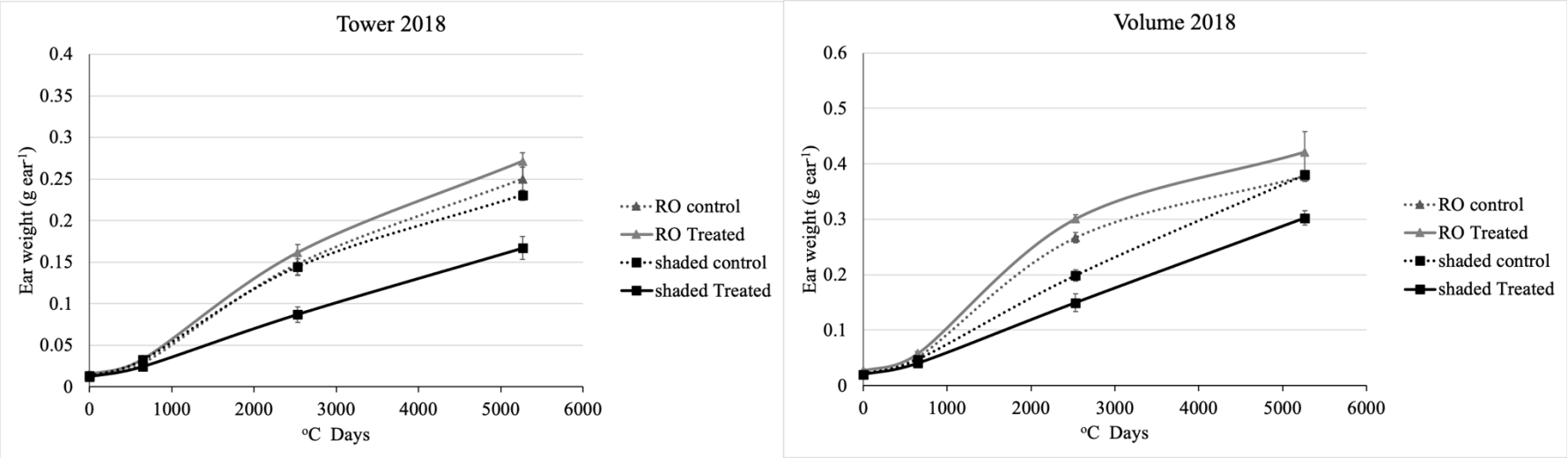

Figure 4-9. Ear weight per shoot plotted against thermal time (ºC days) during the treatment period in 2018. Error bars represent standard error of the mean. Dotted lines represent controls while solid lines represent treated plants. Triangles represent row-opening (RO) treatments, while squares represent shading treatments.

Table 4-4. Effects of pre-anthesis row-opening (RO) on the total and ear biomass per shoot (g) at anthesis. Means, p values and LSD's were produced from ANOVA anaylsis.

Row-opening									
		Ear biomass				Total biomass			
Variety	**Treatment**	**2017**		**2018**		**2017**		**2018**	
Tower	**Control**	0.27		0.25		1.55		1.27	
Tower	**RO**	0.31		0.27		1.73		1.40	
Volume	**Control**	0.51		0.38		2.28		1.51	
Volume	**RO**	0.53		0.42		2.51		1.67	
Variety Mean	**Tower**	0.29		0.26		1.64		1.34	
	Volume	0.52		0.40		2.40		1.59	
Treatment mean	**Control**	0.39		0.31		1.92		1.39	
	RO	0.42		0.35		2.12		1.54	
Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	<0.001	0.04	0.003	0.05	<0.001	0.12	0.058	ns
Treatment (T)	**1**	0.069	ns	0.220	ns	0.010	0.13	0.114	ns
V*T	**1**	0.760	ns	0.655	ns	0.677	ns	0.911	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-5. Effects of pre-anthesis shading on the total and ear biomass per shoot (g) at anthesis. Means, p values and LSD's were produced from ANOVA anaylsis.

Shading									
		Ear biomass				Total biomass			
Variety	**Treatment**	**2017**		**2018**		**2017**		**2018**	
Tower	**Control**	0.27		0.23		1.52		1.14	
Tower	**Shaded**	0.22		0.17		1.36		0.91	
Volume	**Control**	0.53		0.38		2.42		1.62	
Volume	**Shaded**	0.40		0.30		1.85		1.28	
Variety Mean	**Tower**	0.25		0.20		1.44		1.02	
	Volume	0.47		0.34		2.13		1.45	
Treatment mean	**Control**	0.40		0.31		1.97		1.38	
	Shaded	0.31		0.24		1.60		1.10	
Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.001	0.05	<0.001	0.03	0.003	0.26	0.008	0.21
Treatment (T)	**1**	0.013	0.06	<0.001	0.02	0.014	0.25	<0.001	0.08
V*T	**1**	0.135	ns	0.427	ns	0.087	ns	0.168	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-6. Effects of pre-anthesis row-opening on the proportion of biomass partitioned to the ear, leaf and stem. Means, p values and LSD's were produced from ANOVA anaylsis.

		Row-opening					
		Ear biomass ratio		Leaf biomass ratio		Stem biomass ratio	
Variety	**Treatment**	**2017**	**2018**	**2017**	**2018**	**2017**	**2018**
Tower	**Control**	0.178	0.198	0.148	0.157	0.674	0.670
Tower	**RO**	0.178	0.193	0.151	0.145	0.672	0.685
Volume	**Control**	0.223	0.251	0.159	0.167	0.618	0.621
Volume	**RO**	0.212	0.253	0.163	0.149	0.625	0.603
Variety Mean	**Tower**	0.178	0.195	0.149	0.151	0.673	0.678
	Volume	0.218	0.252	0.161	0.158	0.621	0.612
Treatment mean	**Control**	0.201	0.224	0.153	0.162	0.646	0.645
	RO	0.195	0.223	0.157	0.147	0.648	0.644

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.020	0.028	0.002	0.017	0.145	ns	0.250	ns	<0.001	0.012	0.037	0.058
Treatment (T)	**1**	0.208	ns	0.886	ns	0.365	ns	0.078	ns	0.746	ns	0.943	ns
V*T	**1**	0.212	ns	0.626	ns	0.831	ns	0.698	ns	0.440	ns	0.313	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-7.Effects of pre-anthesis shading on the proportion of biomass partitioned to the ear, leaf and stem. Means, p values and LSD's were produced from ANOVA anaylsis.

		Shading					
		Ear biomass ratio		Leaf biomass ratio		Stem biomass ratio	
Variety	**Treatment**	**2017**	**2018**	**2017**	**2018**	**2017**	**2018**
Tower	**Control**	0.179	0.203	0.152	0.162	0.670	0.635
Tower	**Shaded**	0.132	0.183	0.182	0.192	0.685	0.625
Volume	**Control**	0.220	0.236	0.160	0.176	0.621	0.588
Volume	**Shaded**	0.216	0.236	0.181	0.191	0.603	0.573
Variety mean	**Tower**	0.155	0.193	0.167	0.177	0.678	0.630
	Volume	0.218	0.236	0.170	0.183	0.612	0.581
Treatment mean	**Control**	0.199	0.219	0.156	0.169	0.645	0.611
	Shaded	0.174	0.210	0.182	0.192	0.644	0.599

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.061	ns	0.014	0.026	0.382	ns	0.362	ns	0.037	0.058	0.011	0.028
Treatment (T)	**1**	0.198	ns	0.046	0.010	0.008	0.017	0.007	0.014	0.943	ns	0.017	0.009
V*T	**1**	0.269	ns	0.039	0.024	0.525	ns	0.221	ns	0.313	ns	0.521	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

4.3.4 Carpel weight at anthesis in the middle portion of the ear.

Central spikelets in Volume and Tower

The interaction between variety and manipulation treatment on carpel weight was not significant for row-opening or shading in either 2017 or 2018 ($p>0.05$) (Table 4-8 and The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-9). Averaged across varieties shading decreased carpel weight by 55% and row-opening increased carpel weight by 32% in 2017 ($p<0.05$). In 2018 the effects were smaller (33% for shading and 27% for row opening) ($p>0.05$). There was no difference in the weight of carpels from the central spikelet positions in Volume and Tower in any manipulation/year combinations ($p<0.05$).

Central V lateral spikelets in Volume only

The interaction between spikelet position and manipulation treatment on carpel weight in Volume was not significant in either year ($p<0.05$) (Table 4-10 and Table 4-11). Shading decreased carpel weight by 50% in 2017 ($p<0.05$) and 42% in 2018 ($p=0.077$), while row-opening significantly increased carpel weight by 22% ($p<0.05$). There was no significant effect of row opening in 2018. Carpels in the central spikelet positions were significantly ($p<0.05$) heavier than those in the lateral positions in all manipulation/year combinations except the shading experiment in 2017 where the difference was only 20% ($p>0.05$).

Table 4-8. Effects of pre-anthesis shading on indiviudal carpel weight of central spikelets at the mid-portion of the ear at anthesis (mg carpel^{-1}). Means, p values and LSD's were produced from split-plot ANOVA anaylsis.

Shading					
Variety	**Pre-anthesis treatment**	**2017**		**2018**	
Tower	**Control**	0.32		0.19	
Tower	**Shaded**	0.15		0.14	
Volume	**Control**	0.33		0.24	
Volume	**Shaded**	0.14		0.14	
Variety mean	**Tower**	0.23		0.17	
	Volume	0.23		0.19	
Treatment mean	**Control**	0.32		0.21	
	Shaded	0.14		0.14	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.986	ns	0.495	ns
Treatment (T)	**1**	<0.001	0.06	0.062	ns
V*T	**1**	0.778	ns	0.495	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-9. Effects of pre-anthesis row-opening (RO) on indiviudal carpel weight of central spikelets at the mid-portion of the ear at anthesis (mg carpel^{-1}). Means, p values and LSD's were produced from split-plot ANOVA anaylsis.

Row-opening					
Variety	**Pre-anthesis treatment**	**2017**		**2018**	
Tower	**Control**	0.32		0.21	
Tower	**RO**	0.40		0.30	
Volume	**Control**	0.28		0.29	
Volume	**RO**	0.40		0.34	
Variety mean	**Tower**	0.36		0.25	
	Volume	0.34		0.32	
Treatment mean	**Control**	0.30		0.25	
	RO	0.40		0.32	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.741	ns	0.144	ns
Treatment (T)	**1**	0.007	0.05	0.149	ns
V*T	**1**	0.334	ns	0.638	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-10. The effect of spikelet position and pre antheisis shading on individual carpel weight at antheisis (mg carpel^{-1}) of spikelets from the middle portion of the ear of variety Volume. Means, p values and LSD's were produced from split-plot ANOVA anaylsis

Shading					
Pre-anthesis treatment	**Position**	**2017**		**2018**	
Control	**Central**	0.33		0.24	
Control	**Lateral**	0.27		0.14	
Shaded	**Central**	0.15		0.14	
Shaded	**Lateral**	0.14		0.08	
Treatment mean	**Control**	0.30		0.19	
	Shaded	0.15		0.11	
Position mean	**Central**	0.24		0.19	
	Lateral	0.20		0.11	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Treatment (T)	**1**	0.020	0.11	0.077	ns
Position (P)	**1**	0.149	ns	0.014	0.06
T*P	**1**	0.384	ns	0.506	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-11 The effect of spikelet position and pre antheisis row opening on individual carpel weight at antheisis (mg carpel^{-1}) of spikelets from the middle portion of the ear of Volume. Means, p values and LSD's were produced from split-plot ANOVA anaylsis

Row-opening					
Pre-anthesis treatment	**Position**	**2017**		**2018**	
Control	**Central**	0.30		0.29	
Control	**Lateral**	0.25		0.20	
RO	**Central**	0.38		0.34	
RO	**Lateral**	0.28		0.20	
Treatment mean	**Control**	0.27		0.25	
	RO	0.33		0.27	
Position mean	**Central**	0.34		0.32	
	Lateral	0.26		0.20	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Treatment (T)	**1**	0.044	0.05	0.541	ns
Position (P)	**1**	0.050	0.08	0.020	0.09
T*P	**1**	0.414	ns	0.574	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

4.3.5 Mean grain weight (MGW)

MGW was higher in the bottom compared to the top half of the ear in all manipulation/year combinations (data not presented). The purpose of this analysis was to test if the pre-anthesis manipulations (shading and row-opening) affected the top and the bottom half of the ear differently. The interaction between pre-anthesis manipulation and top or bottom half was not significant for any of the manipulation/year combinations ($p>0.05$). Therefore for comparisons with de-grained ears MGW from the bottom half of the control ears were used for the analysis.

There was no effect of either pre-anthesis shading or row-opening on the MGW in either Tower or Volume ($p>0.05$). Nor was there a variety x treatment interaction (Table 4-12 and Table 4-13). Tower had a significantly higher overall MGW compared to Volume ($p<0.05$) in both row-opening and shading experiments in each year. Post-anthesis de-graining treatment did not significantly affect MGW in any of the manipulation/year combinations ($p<0.05$). There were no further significant two or three way interactions.

4.3.6 Grains ear^{-1}

There was no effect ($p>0.05$) of pre-anthesis shading or row opening on the number of grains ear^{-1} in either Tower or Volume (Table 4-14 and Table 4-15). Nor was there a variety x treatment interaction ($p>0.05$). Volume had a significantly larger number of grains ear^{-1} on main shoots compared to Tower ($p<0.05$).

4.3.7 The effect of spikelet position on final grain weight from the middle portion of the ear of Volume and comparison of central spikelet positions in both varieties.

Spikelet position had a significant effect on the weight of grains at harvest with grains of central spikelets being significantly heavier than those at the lateral positions ($p<0.05$). Pre-anthesis shading and row opening had no significant effect on grain weight at either spikelet position (Table 4-16 and *The residual d.f were 3 and 6 for the main plot and sub-plot respectively*

Table 4-17). There were no further interactions.

In no manipulation/year did the central spikelet from the mid portion of the ear in Volume reach a similar weight to that of the central position in Tower ($p>0.05$) (Table 4-18).

Table 4-12. Effects of pre-anthesis shading and post-anthesis de-graining on MGW (mg 100% DM) for grains in the bottom of the ear. Means, p values and LSD's were produced from split-plot ANOVA anaylsis. C= non-de-grained, D = de-grained.

Shading						
Variety	**Shade**	**Post-anthesis de-grain**	**2017**		**2018**	
Tower	**Control**	C	55.84		49.16	
Tower	**Control**	D	56.42		51.25	
Tower	**Shaded**	C	53.33		51.53	
Tower	**Shaded**	D	53.40		51.56	
Volume	**Control**	C	44.45		38.55	
Volume	**Control**	D	44.66		40.80	
Volume	**Shaded**	C	46.99		40.42	
Volume	**Shaded**	D	43.23		40.28	
Variety mean	**Tower**		54.75		50.88	
	Volume		44.83		40.01	
Treatment mean	**Control**		50.34		44.94	
	Shaded		49.24		45.95	
Post-anthesis de-graining	**Control**		50.15		44.92	
	De-grain		49.43		45.97	
Significance		**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)		1	<0.001	1.81	0.002	3.48
Treatment (T)		1	0.367	2.78	0.361	ns
De-grain (D)		1	0.492	2.23	0.096	ns
V*T		1	0.195	2.91	0.754	ns
V*D		1	0.324	2.50	0.995	ns
T*D		1	0.296	3.27	0.082	ns
V*T*D		1	0.413	4.02	0.890	ns

The residual d.f were 3, 6 and 12 for the main plot, sub-plot and sub-sub plot respectively

Table 4-13. Effects of pre-anthesis row-opening and post-anthesis de-graining on MGW (mg 100% DM) for grains in the bottom half of the ear. Means, p values and LSD's were produced from split-plot ANOVA anaylsis. C = non de-grained controls, D = de-grained

Row-opening						
Variety	**Pre-anthesis treatment**	**Post-anthesis de-grain**	**2017**		**2018**	
Tower	**Control**	**C**	53.45		51.37	
Tower	**Control**	**D**	55.49		52.14	
Tower	**RO**	**C**	55.25		54.42	
Tower	**RO**	**D**	53.74		52.26	
Volume	**Control**	**C**	44.66		39.82	
Volume	**Control**	**D**	45.73		40.82	
Volume	**RO**	**C**	44.72		38.88	
Volume	**RO**	**D**	45.44		40.77	
Variety mean	**Tower**		54.48		52.55	
	Volume		45.14		40.07	
Treatment mean	**Control**		49.83		46.04	
	RO		49.79		46.58	
Post-anthesis de-graining	**Control**		49.52		46.12	
	De-grain		50.10		46.50	
Significance		**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)		**1**	0.007	4.43	0.001	3.42
Treatment (T)		**1**	0.961	ns	0.669	ns
De-grain (D)		**1**	0.662	ns	0.552	ns
V*T		**1**	0.933	ns	0.421	ns
V*D		**1**	0.812	ns	0.107	ns
T*D		**1**	0.466	ns	0.423	ns
V*T*D		**1**	0.548	ns	0.145	ns

The residual d.f were 3, 6 and 12 for the main plot, sub-plot and sub-sub plot respectively

Table 4-14. Effects of pre-anthesis shading on the number of grains ear^{-1}. Means, p values and LSD's were produced from split-plot ANOVA anaylsis.

Shading					
Variety	**Pre-anthesis treatment**	**2017**		**2018**	
Tower	**Control**	25.4		19.2	
Tower	**Shaded**	21.7		19.7	
Volume	**Control**	58.4		37.3	
Volume	**Shaded**	57.1		36.0	
Variety mean	**Tower**	23.6		19.5	
	Volume	57.8		36.7	
Treatment mean	**Control**	41.9		28.3	
	Shaded	39.4		27.9	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	<0.001	1.9	0.002	5.5
Treatment (T)	**1**	0.352	ns	0.879	ns
V*T	**1**	0.642	ns	0.751	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-15. Effects of pre-anthesis row-opening (RO) on the number of grains ear^{-1}. Means, p values and LSD's were produced from split-plot ANOVA anaylsis.

Row-opening					
Variety	**Pre-anthesis treatment**	**2017**		**2018**	
Tower	**Control**	22.3		19.5	
Tower	**RO**	21.4		19.8	
Volume	**Control**	58.4		35.1	
Volume	**RO**	56.1		34.9	
Variety mean	**Tower**	21.9		19.7	
	Volume	57.3		35.0	
Treatment mean	**Control**	40.4		27.3	
	RO	38.8		27.4	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	<0.001	3.5	0.020	10.9
Treatment (T)	**1**	0.647	ns	0.998	ns
V*T	**1**	0.839	ns	0.893	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-16. The effect of pre-anthesis shading and row-opening on final grain weight (mg 100% DM) at harvest for central and lateral spikelet positions at the middle portion of the ear. Means, p values and LSD's were produced from split-plot ANOVA anaylsis of data from variety Volume.

Shading					
Pre-anthesis treatment	**Position**	**2017**		**2018**	
Control	**Central**	48.9		36.2	
Control	**Lateral**	40.6		30.4	
Treated	**Central**	47.5		39.9	
Treated	**Lateral**	39.6		33.1	
Treatment mean	**Control**	44.8		33.3	
	Treated	43.6		36.5	
Position mean	**Central**	48.2		38.1	
	Lateral	40.1		31.8	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Treatment (T)	**1**	0.699	ns	0.320	ns
Position (P)	**1**	0.002	3.9	<0.001	1.96
T*P	**1**	0.895	ns	0.530	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-17. The effect of pre-anthesis shading and row-opening on final grain weight (mg 100% DM) at harvest for central and lateral spikelet positions at the middle portion of the ear. Means, p values and LSD's were produced from split-plot ANOVA anaylsis of data from variety Volume.

Row-opening					
Pre-anthesis treatment	**Position**	**2017**		**2018**	
Control	**Central**	49.7		40	
Control	**Lateral**	42.6		32.1	
Treated	**Central**	50.1		39.5	
Treated	**Lateral**	40.4		32.7	
Treatment mean	**Control**	46.2		36.1	
	Treated	45.3		36.1	
Position mean	**Central**	49.9		39.8	
	Lateral	41.5		32.4	
Significance	**df**	**P**	**LSD**	**P**	**LSD**
Treatment (T)	**1**	0.596	ns	0.974	ns
Position (P)	**1**	0.003	4.14	<0.001	1.68
T*P	**1**	0.462	ns	0.463	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Table 4-18. Comparing the grain weight (mg) at 100% dry matter from the central spikelet positions in the mid portion of the ear in Volume and Tower for both manipulation treatments. Means, p values and LSD's were produced from ANOVA analysis.

		Row-opening		Shading	
Variety	**Treatment**	**2017**	**2018**	**2017**	**2018**
Tower	**Control**	56.0	53.2	56.7	47.1
Tower	**Treated**	54.0	54.0	50.8	47.9
Volume	**Control**	49.7	40.0	48.9	36.2
Volume	**Treated**	50.1	39.5	47.5	39.9
Variety mean	**Tower**	55.0	53.6	53.8	47.5
	Volume	51.9	47.0	49.9	42.1
Treatment mean	**Control**	52.9	46.6	52.8	41.7
	Treated	52.1	46.8	49.2	43.9

Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.010	2.8	0.002	4.1	0.075	6.5	0.018	6.4
Treatment (T)	**1**	0.549	ns	0.956	ns	0.167	ns	0.295	ns
V*T	**1**	0.386	ns	0.830	ns	0.382	ns	0.486	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

4.3.8 Relationships

Carpel weight

The relationship between carpel weight at the mid-portion of the ear at anthesis and ear growth rate during the three week period before anthesis is presented in Figure 4-10. Carpel weight was positively related to ear growth rate in the lateral spikelets in Volume in both years, and the central spikelets in Volume in 2017 only ($p<0.05$).However, the % of variance in carpel weight accounted for by ear growth rate was low (34-54%). Relationships between carpel weight and ear growth rate for Tower and the central spikelet positions in Volume in 2018 were weak ($0.1<p<0.05$) and accounted for relatively little of the variation in carpel weight (R^2 = 0.19-0.21).

Final grain weight – middle of the ear

Grain weight in the mid portions of the ear at harvest was not significantly related to carpel weight from the same portion of the ear at anthesis. Pre-anthesis shading and row opening treatments plus their respective controls were used to vary carpel weight at anthesis (Figure 4-11).

MGW and grains ear^{-1}

MGW (averaged over entire ear) and the number of grains ear^{-1} was not significantly related to either ear growth rate during the treatment period or ear weight at (Figure 4-12 and Figure 4-13).

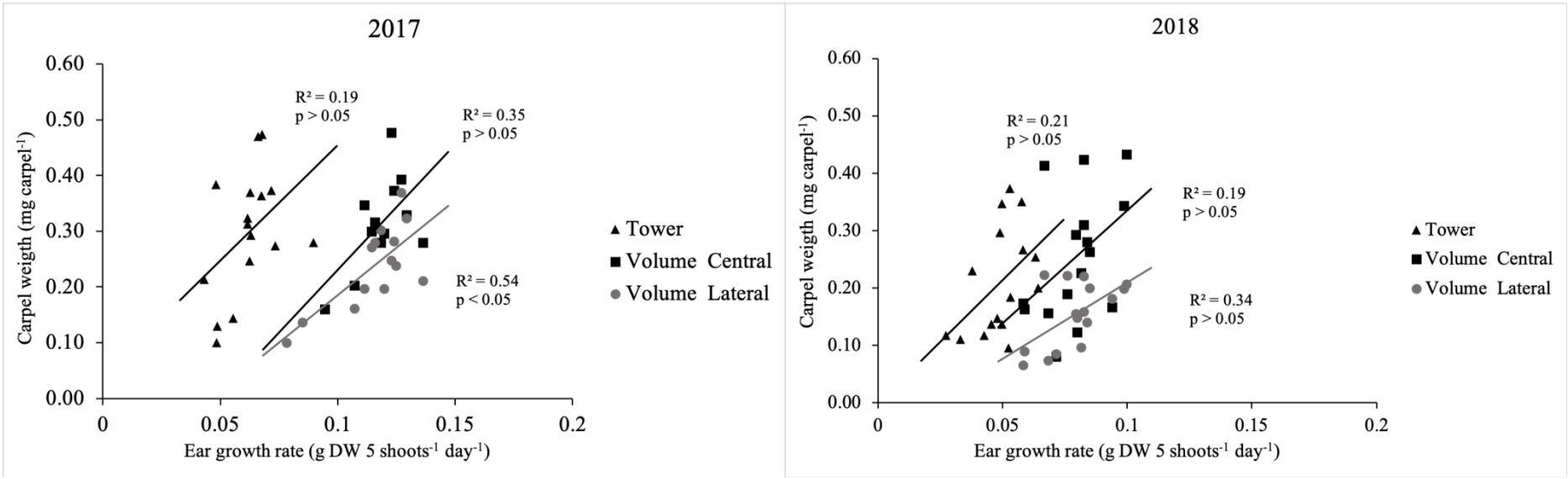

Figure 4-10. The relationship between carpel dry weight (mg carpel^{-1}) in the mid portion of the ear at anthesis and ear growth rate (g DW 5 shoots^{-1} day^{-1}) during the three week period prior to anthesis. Values for Volume are divided into central and lateral spikelet positions while values for Tower are from central positions. P values are produced from simple linear regression.

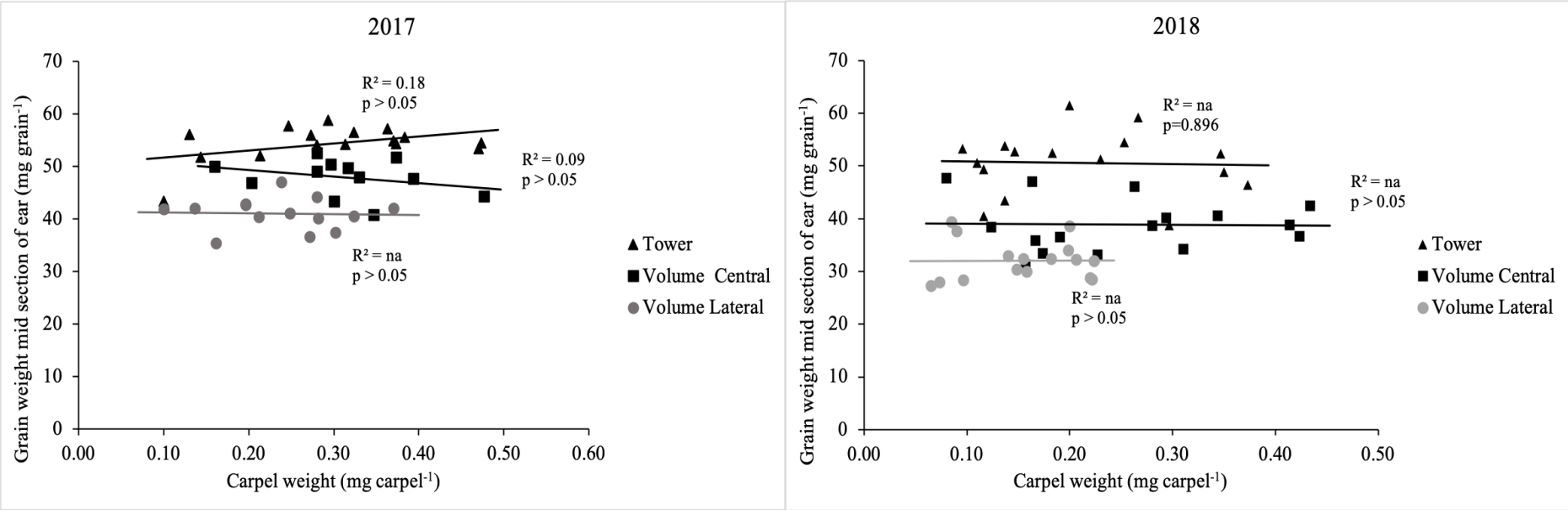

Figure 4-11. The relationship between grain weight in the middle of the ear (mg grain^{-1}) at harvest carpel weight (mg carpel $^{-1}$) at anthesis. Values for Volume are divided into central and lateral spikelet positions while values for Tower are from central positions. P values are produced from simple linear regression.

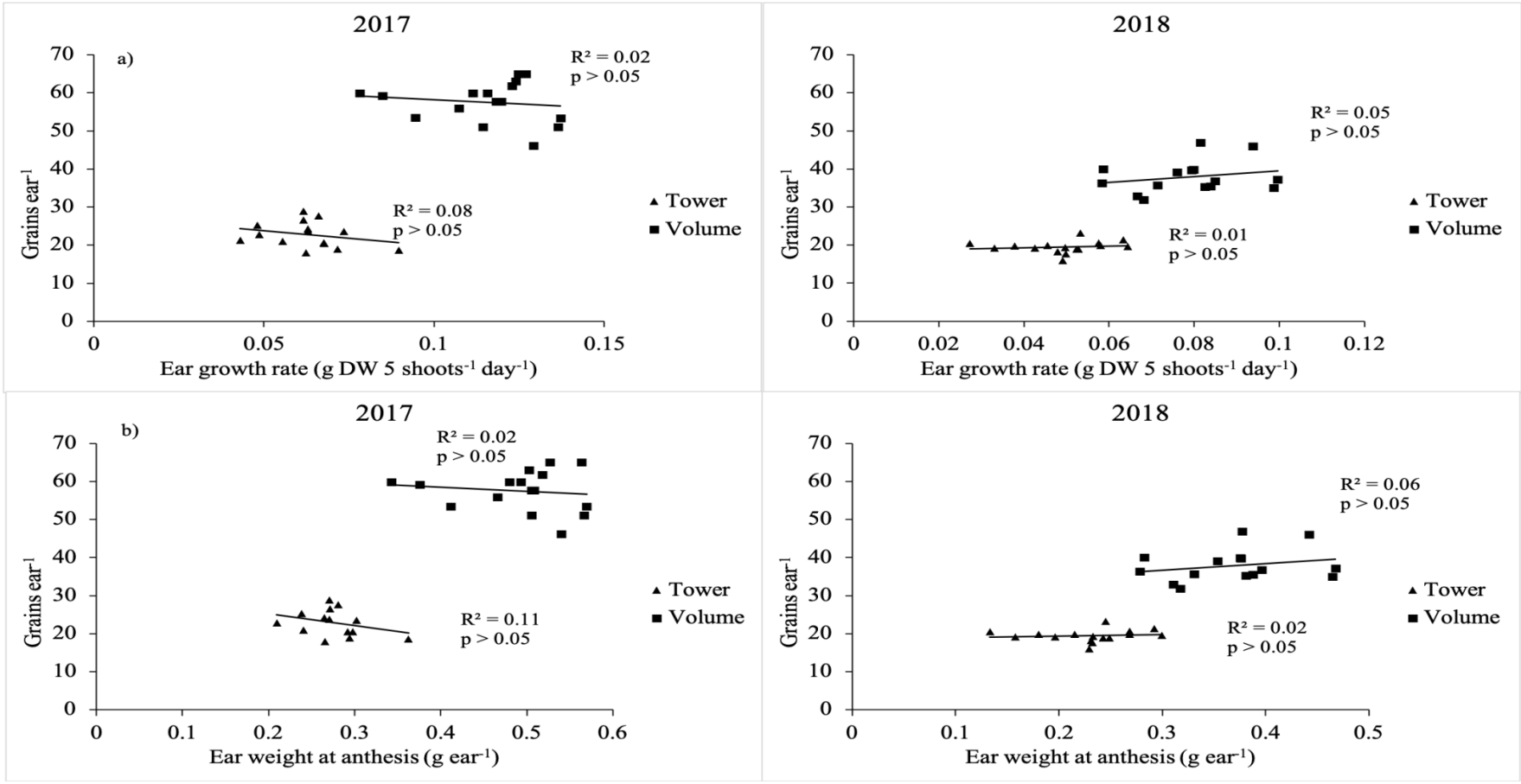

Figure 4-12. The relationship between grains ear^{-1} and a) ear growth rate (g DW 5 shoots^{-1} day^{-1}) during treatment period and b) ear dry weight at anthesis (g ear^{-1}). P values are produced from simple linear regression.

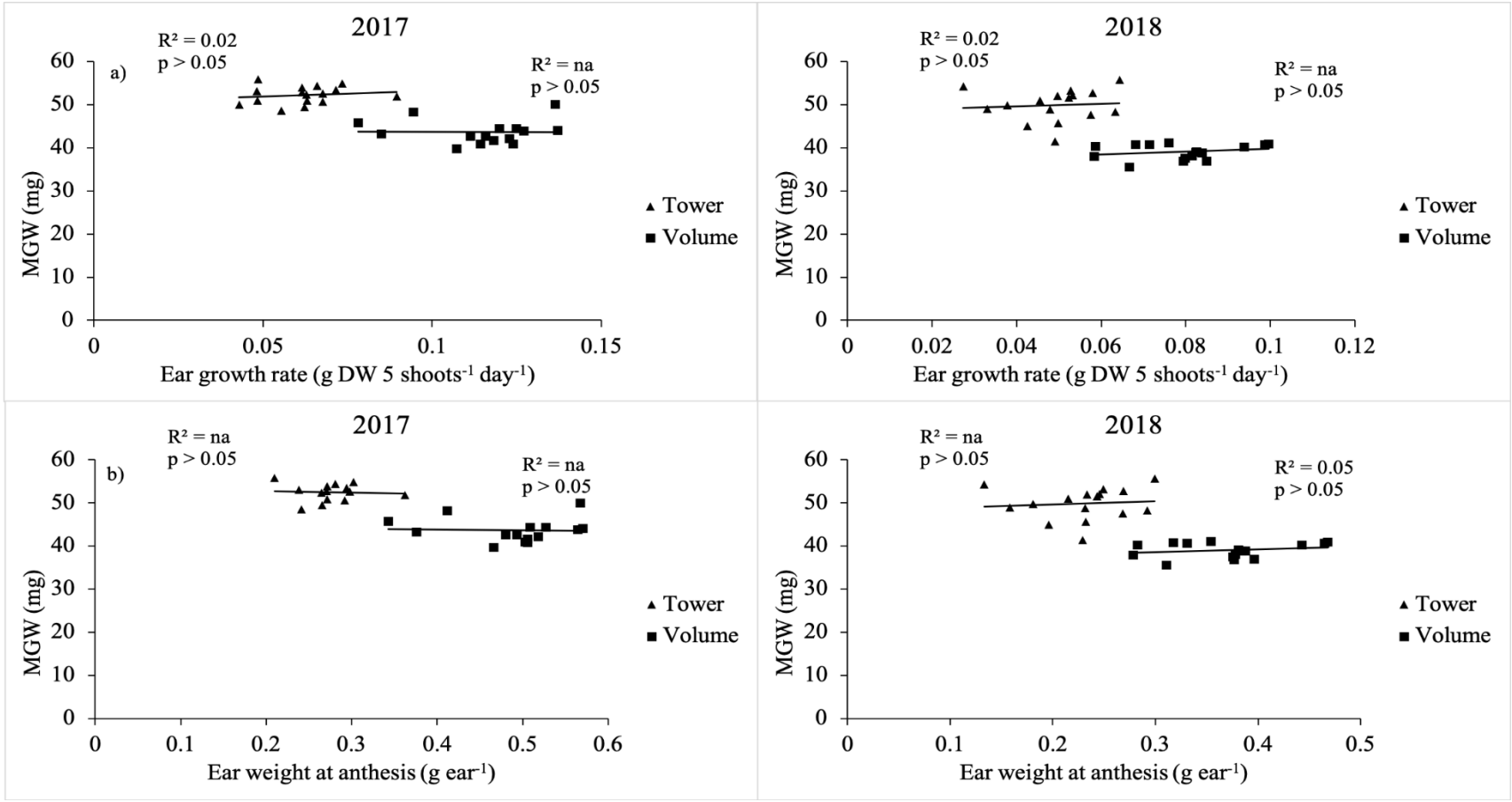

Figure 4-13. The relationship between MGW (mg) at harvest and a) ear growth rate (g DW 5 shoots^{-1} day^{-1}) during treatment period and b) ear dry weight at anthesis (g ear^{-1}). P values are produced from simple linear regression.

4.4 Discussion

Shading and row opening treatments varied PAR availability to the crop during a three week period from flag leaf emergence to anthesis. This treatment period broadly corresponds with the critical period for grain number formation in both six-row and two-row barley varieties reported by Arisnabarreta and Miralles (2008a). Shading reduced PAR interception by approximatley 70% and row opening increased it by 10-24%, resulting in a reduction and increase in ear growth rate of 24% and 10% respectively. Thus shading decreased the amount of biomass in the ear at anthesis in both the six- and two-row variety, while row-opening had more marginal effects. The effects of treatments designed to alter rates of photosynthesis on organ growth can be moderated by changes in the relative dry matter partitioning to different plant organs. Arisnabarreta and Miralles (2008b), found that shading immediately prior to heading of barley reduced ear dry weight in absolute terms, but increased ear weight relative to other plant organs as a larger proportion of the dry matter was allocated to the ear. In the current experiment, effects of shading on relative partitioning tended to be small and inconsistent between years. Interestingly, partitioning to the ear was reduced rather than increased, whilst that to the leaves was increased.

The change in ear growth was associated with corresponding effects on carpel weight at anthesis with shading reducing and row-opening increasing carpel weight. No study has investigated the effect of manipulation of light availability during the late stem extension period on carpel weight in barley, although the results of this study are in agreement with studies carried out on wheat and sunflower (Castillo et al., 2017, Acreche et al., 2009). In the six-row variety Volume, carpels in the lateral spikelet positions were found to be lighter than those in the central positions. In wheat, carpels in florets further from the rachis were found to be lighter than those closer to the rachis (Xie et al., 2015, Hasan et al., 2011, Guo et al., 2016). Grain filling in these more distal florets is also more sensitive to reductions in post-anthesis assimilate availability (Bremner and Rawson, 1978) suggesting that there is competition for resources between florets at different positions. If a similar mechanism of competition occurs between central and lateral spikelets during the development of the ear in six-row barley, it might be expected that carpel weight in the lateral spikelets would be more sensitive to shading than those in central spikelets. However, this was not the case in

this study as carpel weight in both the central and lateral positions responded similarly to changes in light availability during the late stem extension period, suggesting that there is a mechanism controlling the relative assimilate partitioning to both central and lateral positions when supplies become restricted.

Surprisingly there was no significant effect of either pre-anthesis shading or row-opening on grains ear^{-1} at harvest. These results contradict previous studies that have shown pre-anthesis shading to reduce grains ear^{-1} in six-row and two-row barley and wheat (Arisnabarreta and Miralles (2008a), Arisnabarreta and Miralles, 2008b, Acreche et al., 2009). It needs to be noted that the current study focused on tagged main stems without measurements on tillers, it is plausible that in a situation where resources were reduced (shading) or increased (row-opening) that the effects on the main shoot ear may have been diluted by the effects on the tillers. The treatment period coincided with the period of tiller mortality (Kirby et al., 1985, Kennedy et al., 2016), therefore, in the case where PAR was reduced tillers could have been aborted to ensure survival of the main shoot and where PAR was increased tillers that normally would have died could have been retained increasing the demand for resources and diverting resources away from main shoot ear development. If this is indeed the case, it would appear that spikelet fertility and grain numbers on the main shoot ear are maintained in the face of variations in pre-anthesis PAR, whilst carpel weight is not.

There is a widely held view that final grain weight in sink-limited cereal crops is related to carpel weight at anthesis and that carpel size in some way determines the storage capacity of the grain (Guo et al., 2016, Xie et al., 2015, Hasan et al., 2011). Much of the evidence supporting this view has come from correlations between carpel weight and final grain weight across different varieties. However, results from the present study cast doubt on this view. Although carpel weight was varied by shading and row-opening treatments, no significant relationship between carpel weight at anthesis and grain weight at harvest in the mid portion of the ear was found. This finding is supported by a recent study in wheat, where agronomic inputs (seed and N) caused large variations in carpel weight across environments (10 fold), however, only small changes in grain size occurred (0.5 fold) (Benincasa et al., 2017). The authors questioned if grain weight is conservative because of a genetic limitation (sink limitation) or that the plant adjusts grains m^{-2} to match source availability (source limitation).

Similarly, the carpel weight of central spikelets in the mid portion of the ear of Volume and Tower were comparable, yet the final weight of grains at these spikelet locations was lower in Volume than Tower. These results show that carpel weight at anthesis is not tightly coupled to the final grain weight.

Previous work on six- and two-row barley has found no effect of pre-anthesis shading on MGW (Arisnabarreta and Miralles, 2008b), consistent with observations in the current study, although in wheat MGW was increased (Acreche et al., 2009). The authors' reasoning for this increase was that the reduction in grains ear^{-1} from pre-anthesis shading reduced the overall demand for resources during grain filling, thus increasing the availability of assimilates per grain and thus individual grain weight Acreche et al. (2009). The different responses of wheat and barley to pre-anthesis shading outlined above may relate to differences between source and sink limitation of grain filling in the two species as found previously (Serrago et al., 2013).

Grain weight was not limited by source availability during grain filling in this study, as post-anthesis de-graining did not increase grain weight at harvest, therefore, the limitation on grain weight in both a six and a two-row variety was PGW i.e. grain weight was sink-limited. The results of this study suggest that PGW is insensitive to variations in PAR during the late stem extension period and the variations in carpel weight that result suggesting that there is a mechanism controlling the PGW that may not involve assimilate supply.

In the six-row variety Volume, final grain weight at harvest was heavier for grains in the central compared to the lateral positions, although again there was no influence of shading or row-opening during the late stem extension period on grain weight in either spikelet position. The grain weight in the central spikelets of Volume was less than that of the central positions in Tower suggesting that PGW in these positions is inherently lower in Volume compared to Tower. The lower MGW of Volume compared to Tower was, therefore, the result of a lower PGW of grains from both central and lateral spikelets.

It was hypothesised that due to the larger number of spikelets ear^{-1} in a six row variety that ear growth rate and carpel weight in Volume would be more sensitive to variations in pre-heading PAR, and hence likely assimilate supply, compared to the two-row variety, Tower. However, there was no evidence to support this. There was no significant treatment x variety

interaction for ear growth rate or carpel weight implying that the response to variations in incident PAR was comparable in the two varieties.

4.5 Conclusion

Modification of growth conditions via varying light availability during the late stem extension period led to changes in carpel weight at anthesis in both a hybrid six-row and a conventional two-row barley variety. This modification of growth conditions pre-anthesis did not translate into effects on sink capacity in either row-type. Surprisingly the six-row variety was not more sensitive to PAR availability during the late stem extension period compared to a two-row variety. Carpels and grains in the lateral spikelet positions were significantly lighter than those in the central positions, but were no more sensitive to changes in PAR availability.

Chapter 5 **General Discussion**

Global agriculture is faced with the massive challenge of ensuring food security with a rapidly expanding population, while on a more local level, tillage farmers in Ireland are faced with high costs of production and a low commodity price for their grain. Thus, efficiencies to maximise output whilst minimising inputs are vital to ensure both food supply and economic sustainability of the tillage sector on both a global and local level. The main hypothesis set out in this research stemmed from the inherent differences in the yield components of a two- and a six-row winter barley. At the outset of this project, it was postulated that crops with differing yield components may require different disease management strategies depending on whether their yield is limited by the number and storage capacity of the grains produced (sink-limited) or the crop's ability to provide assimilate to fill these grains (source-limited) during grain filling. The introduction of the hybrid six-row varieties has been relatively recent and therefore limited research has been conducted to support current management practices. Moreover, no study has investigated if disease management strategies should differ between two and six-row varieties. Thus, the overall aim of the research presented in this thesis was to establish an understanding of how yield is formed in both two- and six-row winter barley varieties and to utilise this information to target disease management.

5.1 Source versus sink limitation of yield

In barley the importance of sink capacity on yield formation is well established, although the role of potential grain weight (PGW) or grain storage capacity is sometimes forgotten, as many of the previous investigations on sink capacity have focused on the number of grains m^{-2}. It was reasoned that due to the higher number of grains m^{-2} in a six-row variety their sink capacity would be greater than that of a two-row variety. However, this proved to be untrue; in fact the sink capacity of both row types in this study was similar. This is displayed by the results of chapters 3 and 4, when assimilate supply was manipulated both pre- and post-anthesis the response of the row-types did not differ.

The results of this study support the finding that yield of barley is sink-limited (Bingham et al., 2007a), while also adding six-row barley to that understanding as previous work focused on two-row barley. This research, for the first time in the same study, utilised two approaches

to assess the source-sink balance of the crops, those being the manipulation of the soucre:sink ratio during grain filling and the estimation of assimilate supply for grain filling. There are potential uncertainties with both methods, although both methods indicated the same result that the yield was sink limited and that the source-sink balance did not differ between a two-and a six-row winter barley variety. Therefore, with contrasting methods showing the same answer confidence can be taken from the result.

The six-row variety produced a larger number of grains m^{-2} compared to the two-row variety, although yield was similar. This was due to mean grain weight (MGW) in the six-row variety being correspondingly lower. In chapter 2 there was a variance in MGW with site and season, but in all cases the two-row variety had a greater MGW compared to the six-row. This finding is supported by other studies investigating two- and six-row barley (Arisnabarreta and Miralles, 2006, Arisnabarreta and Miralles, 2008a). Evidence in the present study shows that the lower MGW of the six-row variety was not due to a source-limitation of grain filling but was the result of an inherently lower PGW. In chapter 3 de-graining removed any source-limitation of grain filling yet, in the absence of source limitation, MGW in Volume failed to reach values of the two-row variety Tower. It could be argued that the lighter grains in the lateral spikelet positions are the cause of this lower MGW in Volume (as MGW is an average of grains from all spikelet positions). However, in chapter 4 this argument was refuted as it was shown that grains in the central spikelet positions in Volume were also significantly lighter than grains in the same central positions in Tower, suggesting that there is a genetic control on PGW. This genetic control could involve the potential interplay between the number of grains m^{-2} and PGW.

5.2 Control of seed size

The objective of any flowering crop is to produce seed for future generations. In plants the survival of the offspring relies on the fitness of their parents to produce seed with an adequately sized embryo and an endosperm to provide assimilate for early growth. It has been established that MGW is generally more conservative than grains m^{-2}, with the latter varying more widely across sites and seasons than MGW (Sadras, 2007, Quintero et al., 2018, Kennedy et al., 2016). Adjusting the number of grains produced to match the potential of the plant to supply assimilates for filling those grains would enable a range of viable grain weights to be produced. However, it is well documented that MGW can be reduced if

extreme conditions restrict photosynthetic activity during grain filling, possibly because assimilate supply is insufficient to meet the sink capacity. Some authors have highlighted that there may be a trade-off between these two components under these types of conditions such that MGW is reduced when grain numbers are increased (Sadras, 2007, Bulman et al., 1993, Gambín and Borrás, 2010, Acreche and Slafer, 2006, Quintero et al., 2018).

The mechanisms controlling PGW and how grain numbers may be adjusted to maintain PGW remain unclear. The period when grain number is determined is well defined as the period close to heading in both two and six-row barley (Arisnabarreta and Miralles, 2008a). Grain numbers are determined prior to anthesis and during rapid stem extension through tiller survival, spikelet and floret survival and the success of fertilisation. There is no evidence of post-anthesis grain abortion in barley (Kennedy et al., 2018). By contrast, when PGW is determined is less clear. There is evidence in the literature that it might be controlled by pre and/or early post-anthesis development.

It was previously understood that carpel weight at anthesis and MGW at harvest were closely related (Scott et al., 1983, Hasan et al., 2011, Xie et al., 2015). However, results in chapter 4 show that this is not the case for either two- or six-row barley. Studies where this relationship has been found for the most part varied carpel weight by comparing genotypes with large and small grains. In the present study light availability was used to modify pre-anthesis growth and carpel weight suggesting that the relationships reported previously may have been a correlation and not causal. Therefore, other mechanisms must control seed size. Physical limitations, setting a upper limit on grain size during grain filling has been shown in rice (Lombardo and Yoshida, 2015) where the palea and lemma form a tight-fitting enclosure that restricts grain growth during grain filling, defining potential size before the grain has formed. In wheat the size of the floral cavity which is defined by glume, lemma and palea has been shown to have a strong relationship with final grain weight ($r^2 = 0.65$) ((Millet and Pinthus, 1984, Millet, 1986). Further to the potential physical limitation, evidence of communication between the seed coat and the endosperm in early grain development has been presented (Brinton and Uauy, 2018) as evidence in *Arabidopsis* which suggests that the seed coat can be increased in size indirectly to accommodate growth in the endosperm (Garcia et al., 2005). Grain weight in cereals has been related to the number of endosperm cells formed in the period immediately post-anthesis (Cochrane and Duffus, 1981). There is recent evidence that maternal tissues may help regulate endosperm

development. It has been shown that timely programmed cell death (PCD) in the pericarp allows for the supply of nutrients to fuel cell formation and allowing for space within the endosperm for cells to form (Volodymyr et al., 2018).

All of the above mentioned evidence would indicate that the control of grain weight is not just a simple relationship between carpel weight at anthesis, there are a complex of relationships and signals which govern grain weight. Although what can be concluded from the current study is that seed weight is sink-limited. It is clear the PGW of barley is a limiting factor on yield. Therefore, in order to raise yield potential an improved understanding of the control of PGW is required. Efforts to better understand seed size are being made in wheat (Brinton and Uauy, 2018) and rice (Li and Li, 2015) with new techniques being utilised such as genome sequencing and gene editing. If an improved understanding of the control of seed size occurs in this crop species, it is plausible to apply similar techniques in barley. Increasing the PGW of barley will almost certainly increase yield, as assimilate supply for grain filling is non-limiting in many environments, while in some cases (2016 in chapter 3) source and sink can be in close balance. Although if PGW is raised by a large amount this will alter the source-sink balance, which could increase the risk of source limitation and the effects of disease on yield.

5.3 Effects of disease and yield response to fungicide

The results of chapters 2 and 3 clearly show that fungicide treatment increased sink capacity. Grain number m^{-2} and PGW were greater in fungicide treated crops than untreated crops. As healthy area light interception was also increased by fungicide treatment the net effect was that there was no difference in the source-sink balance between treated and untreated crops as fungicide treatment increased the assimilate available for grain filling in line with the greater demand. There were significant effects of fungicide treatment on disease control during the pre-anthesis period (GS31-GS55) in both chapters 2 & 3, although in chapter 3 this control of disease had very small effects on the amount of light intercepted by healthy tissue pre-anthesis. The severity of disease during this period was relatively low and the majority of the disease which was present in the canopy pre-anthesis was located on lower leaves therefore having a small impact on the amount of light intercepted. Any yield response to fungicide could involve effects resulting from the control of disease or other more direct effects on host physiology. The small effects of disease (and conversely fungicide treatment)

on light interception suggests increases in grain number and PGW could arise from direct effects of fungicide. There has been evidence of such effects in work carried out in spring barley, where in the absence of visible disease that the application of azole and QoI fungicide groups resulted in increased grain numbers (Bingham et al., 2014, Bingham et al., 2012)

In chapter 2 different components of sink capacity were increased by fungicide treatment in both varieties. When a variety x fungicide interaction occurred in both MGW and grains m^{-2} it was caused by grains m^{-2} being more responsive to fungicide in the six-row variety and MGW being more responsive in the two-row variety. Where these interactions occurred, there was also, in some cases, a variety x fungicide interaction for the severity of disease, although as stated these interactions were caused by differing levels of disease in the untreated and 1 spray programme with disease levels being similar when a more robust fungicide programme was applied. This suggests that the fungicide either through the control of disease or possible through direct effects on the plant affected different components of sink capacity.

In chapter 2 the yield response to fungicide timing of both row-types was investigated. It was expected that due to the higher number of grains m^{-2} in a six-row variety that it would behave more like a wheat crop in terms of fungicide timing than a two-row variety. That being that protection from loss of green area by disease infection would be required later into grain filling. Before this research was conducted GS49 (awn emergence) was recommended as the final fungicide timing in winter barley (Glynn and Grace, 2017). In the first set of experiments a significant response was seen to a fungicide timing applied to the ear, this was attributed to the decline in sensitivity of ramularia to the SHDI's, QoI's and azole fungicide groups. In other experiments when ramularia was effectively controlled at GS49 through the application of a multi-site fungicide the response to fungicide at GS65 was not observed. Despite differences in disease control, both two- and six-row varieties responded similarly to fungicide timing, indicating that there is no requirement to alter disease management strategy based on row-type. This is explained by their comparable source-sink balance.

An unexpected finding in chapter 2 was the effect that fungicides had on the level of straw breakdown (brackling) that occurred in both varieties. It was clear that where fungicide was applied at GS31/32 and GS49, the level of straw breakdown was reduced compared to the

untreated programme. The cause of this effect is not known, and its investigation was beyond the scope of this study. However, both the control of disease and possible direct effects of the fungicide on stem growth and tissue structure cannot be ruled out. The products applied at the mentioned timings were a mix of three active ingredients, an azole, an SDHI and a QoI (epoxiconazole, fluxapyroxad and pyraclostrobin respectively). While some companies market fungicide products claiming direct structural effects there is a lack of evidence in the published literature to support this claim. Moreover, there is a general lack of evidence on the effects of fungal pathogens on the strength of straw. This is an obvious area of future research as straw breakdown is of concern for growers of all cereals especially barley and oats. This is because straw is used for livestock and is thus a valuable commodity in mixed farming areas.

5.4 Future of disease management and implications of findings

Disease management is an essential part of crop management in cool temperature climates as there is adequate moisture and temperature for fungal pathogen to grow. In this study when disease pressure was high the yield was nearly doubled by the use of fungicides (chapter 2). However, pesticides in general are coming under increased regulatory pressures with a number of important actives being removed from the market in recent years, such as the recent removal of chlorothalonil, which in this study was shown to be extremely important in the control of ramularia. Fungicides must be used as part of an integrated pest management (IPM) based strategy with non-chemical means being utilised to control these fungal pathogens. However, crops grown in this study were subject to best practice including rotation, sowing date and seeding rate to best limit the risk of disease infection and still significant yield loss from disease infection occurred. There is no doubt that policy pressures will mean that less fungicide will be applied to crops in the future, therefore the need to optimise current timings has never been more important.

Commercially winter barley is generally grown using a three spray programme, those timings being mid-to-late tillering (GS25-29), early stem-extension (GS31/32) and awn emergence (GS49). The key timings in the present study were GS31/32 and GS49, but the requirement of the GS25-29 timing is dependent on season and disease pressures. The rationale behind this timing is to ensure tiller survival, as the number of ears m^{-2} has been

shown to be the key determinate of spring barley yield (Kennedy et al., 2016). Moreover, disease has been shown to reduce tiller production (Lim and Gaunt, 1986), although this evidence relates to one disease (powdery mildew) in controlled environments. In reality in barley crops during the early spring there can be a number of disease present as was reported in chapter 2. When comparing the 2 and 3 spray programmes in chapter 2 at only two of the six site- seasons were the yield response to the GS25-29 timing significant. Although this may be an unfair comparison as different fungicide products were applied at these timings, they did, however reflect a commercial programme, questioning as to what governs the importance of this timing. What impact is disease during this period having on tiller survival? Only at one site/season in chapter 2 was there a significant effect of fungicide treatment on the number of ears m^{-2} and at this site/season there was no difference between the 2 and the 3 spray programme. This would suggest that the GS25-29 timing has no impact on the number of ears m^{-2} present at harvest. However, the types of disease present at this timing must be taken into account, for example the impact that net blotch would have on the crop at this time may be significantly different to that of mildew. These are all questions a grower must account for when deciding whether or not to apply fungicide. There are however unanswered questions as to the impact of disease and the type of the disease on yield during this period. If this timing is not having an impact on the survival of tillers then there may be a case for the omittance of the timing from commercial programmes.

This study also refuted the need for fungicide applications post GS49, which in some cases would be carried out commercially for the reason for protecting the canopy late into grain filling. In this study there is a weight of evidence to point towards applications later than GS49 not being required. Therefore, if we were to take a 4 spray programme often used commercially, potentially 2 of those timings, the mid-tillering and the post GS49 ear spray could be dropped out of the programme without a significant yield penalty. This would reduce both cost and the fungicide usage on the crop.

The results of this study can be incorporated into an IPM based strategy, as the physiological information about when yield is formed to best target fungicide timing has been shown in both a two-row and for the first time a six-row winter barley variety. This information in conjunction with experiments in chapter 2 show the optimal disease management strategy for both row-types, with control of disease targeted during the formation of sink capacity. However, the potential for direct physiological effects of fungicide question the current IPM

based strategy for the use of fungicides. Currently fungicides should only be applied when a yield or quality benefit is expected, with disease monitoring playing an important role in the decision to apply a fungicide or not. If fungicides are having a direct effect on sink capacity and straw strength, it is plausible that the application of fungicide may increase yield even when disease levels are low. However, if the mechanism by which fungicides impact sink capacity are better understood, it may be possible to get the same effects with non-chemical products, such as plant bio-stimulants or elicitors. Avenues for further investigation could involve reducing plant stress through the use of some of these non-chemical products as some diseases have been shown to be stress induced for example ramularia leaf spot (Havis et al., 2014a). However, the results of these non-chemical products are extremely inconsistent and evidence of more consistent effects will be required before such products can be relied upon for disease control by growers.

5.5 Summary of key findings

The key findings of this research are:

- The response to fungicide timing did not differ between a conventional two-row and a hybrid six-row winter barley variety.
- The source-sink balance of a two and a six-row winter barley variety were similar.
- Fungicide treatment did not alter the source-sink balance as increases in source capacity were accompanied by increases in grain sink capacity
- Sink capacity in both a two and a six-row variety was insensitive to variations in light availability during the late stem extension period.
- Carpel weight at anthesis was not related to grain weight at harvest.

5.6 Key recommendations

- Disease control programmes designed for two-row winter barley are also suitable for six-row varieties.
- Disease should be controlled via applications of fungicide at GS31/32 and GS49 in both two- and six-row winter barley varieties.
- Fungicide applications after ear emergence are not required to maximise yield regardless of disease pressure.

- There may be opportunities to omit applications at GS25-29 depending on the severity and type of disease observed in the crop as yield responses to this timing are infrequent
- There is need to better understand the control of potential grain weight in order to increase the yield potential of barley.

Chapter 6 **References**

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Appendix 1 Presentations, articles and posters

Beattie, R., Spink, J., Bingham, I. 23th March 2016. Understanding the control of yield formation in two- and six-row winter barley varieties to target disease managementOral presentation at the SRUC Postgraduate Research Conference, Edinburgh, UK.

Beattie, R., Spink, J., Bingham, I. 22th March 2017. Do two- and six-row winter barley varieties differ in their source-sink balance during grain filling? Poster presentation at the SRUC Postgraduate Research Conference, Edinburgh, UK.

Beattie, R. J., Spink, J. H., 22nd June 2017. Winter barley agronomy: two- and six-row. News article in the Irish farmers Journal, Dublin.

Beattie, R., Spink, J., Finnan, J., Bingham, 28th June 2017. Winter barley agronomy: two- and six-row. Oral and poster presentations to various groups of growers, agronomists and others at the Teagasc Oak Park Crops Research Centre Open Day 2017, Carlow, Ireland.

Beattie, R., Spink, J., Finnan, J., Bingham, I. 31st January 2018. Does a six- and a two-row winter barley variety need to be treated differently? Conference paper and presentation at the Teagasc National Tillage Conference 2018.

Beattie, R., Spink, J., Finnan, J., Bingham, I. 7st February 2018. Does a six- and a two-row winter barley variety need to be treated differently? Oral presentation to a group of undergraduate agricultural students at Teagasc, Oak Park, Carlow, Ireland

Beattie, R., Spink, J., Finnan, J., Bingham, I. 19th February 2018. Understanding the control of yield formation in two- and six-row winter barley varieties to target disease management. Oral presentation as part of the Student Seminar Series, Oak Park, Carlow, Ireland.

Beattie, R., Spink, J., Finnan, J., Bingham, I. 27th February 2018. Understanding the control of yield formation in two- and six-row winter barley varieties to target disease management. Paper and conference presentation. The Dundee Conference. Crop Protection in Northern Britain 2018.

Beattie, R., Spink, J., Finnan, J., Bingham, I. 13th March 2018. Do two- and six-row winter barley varieties differ in their source-sink balance during grain filling? Poster presentation at the Teagasc SRUC Joint Conference, Edinburgh, UK.

Beattie, R., Spink, J., J., Finnan, Bingham, I. 21th March 2018. Understanding the control of yield formation in two- and six-row winter barley varieties to target disease management.Oral presentation at the SRUC Postgraduate Research Conference, Edinburgh, UK.

Beattie, R., Spink, J., J., Finnan, Bingham, I. 5th September 2018. Do a two and a six-row winter barley variety require different disease management strategies? Oral presentation at the Crops, Environment and Land use Programme Walsh Fellow regional competition, Oak Park, Carlow, Ireland.

Beattie, R., Spink, J., J., Finnan, Bingham, I. 5th October 2018. Do a two and a six-row winter barley variety require different disease management strategies? Poster presentation at the Teagasc Walsh Fellowship Seminar, Johnstown Castle, Wexford, Ireland.

Beattie, R., Spink, J., J., Finnan, Bingham, I. 30th January 2019. Do a two and a six-row winter barley variety require different disease management strategies? Poster presentation at the Teagasc National Tillage Conference 2018, Kilkenny, Ireland

Beattie, R., Spink, J., J., Finnan, Bingham, I. 10th April 2019. Crop Protection: the challenge of finishing winter barley. News article in the Crop protection magazine insert in the Irish Farmers Journal, Dublin, Ireland.

Beattie, R. J., Spink, J. H., 20nd June 2019. Winter barley agronomy: two- and six-row. News article in the Irish farmers Journal, Dublin.

Beattie, R., Spink, J., Finnan, J., Bingham, 26th June 2019. Winter barley agronomy: two- and six-row. Oral and poster presentations to various groups of growers, agronomists and others at the Teagasc Oak Park Crops Research Centre Open Day 2017, Carlow, Ireland.

Spink, J., Beattie, R., Glynn, E. 9th February 2017. Maximising winter barley yields. Oral presentation delivered by John Spink at the BASF technical conference Kilkenny, Ireland.

Spink, J., Beattie, R., 1st February 2018. A review of the barley agronomy project. Oral presentation delivered by John Spink at the BASF technical conference Kilkenny, Ireland.

Spink, J., Beattie, R.,. 7th February 2019. Barley agronomy - A review of the barley agronomy project. Oral presentation delivered by John Spink at the BASF technical conference, Kilkenny, Ireland.

Appendix 2 Crop Agronomy

2015

Treatment	Site	
	Teagasc	SRUC
Sowing date	2/10/2014	18/09/2014
Insecticide	5/11/2014 Sparviero 50 ml ha^{-1}	20/10/2014 Clayton Sparta 150 ml ha-1
Herbicide	5/11/2014 Dff 0.25 l ha^{-1} Croplink IPU 2.0 14/04/2015 Axial 0.25 l ha^{-1} Adigor 1.0 l ha^{-1}	1/10/2014 Picona 3.0 l ha^{-1} 13/04/2014 Ally 10 g ha^{-1} 8/05/2015 Gala 0.75 l ha^{-1}
Fertiliser	18/02/2015 0:7:30 450 kg ha^{-1} 6/03/2015 Split 1 2/04/2015 Split 2	01/09/14 P_2O_5 60 kg ha^{-1} K_2O 60 kg ha^{-1} 11/03/2015 N split 1 17/04/2015 N split 2
Fungicide	GS25 27/03/2015 GS31/32 16/04/2015 GS49 13/05/2015 GS65 25/05/2015	GS25 19/03/2015 GS31/32 20/04/2015 GS49 08/05/2015 GS65 20/05/2015
Growth regulator	GS30 8/04/2015 GS37 1/05/2015	GS30 16/04/2015 GS37 8/05/2015

2016

Treatment	Site	
	Teagasc	SRUC
Sowing date	30/09/2015	18/06/2015
Insecticide	3/11/2015 Sumi Alpha 165 ml ha^{-1}	12/10/2015 Sparta 100 ml ha^{-1} 26/10/2015 Sparta 100 ml ha^{-1}
Herbicide	3/11/2015 Sempra 0.25 l ha^{-1} Croplink IPU 2.0 l ha^{-1} 21/03/2016 Axial 0.25 l ha^{-1} Adigor 1.0 l ha^{-1}	5/10/2015 Picona 3.0 l ha^{-1} 20/04/2016 Ally 10 g ha^{-1} Starane 1.0 l ha^{-1}1
Fertiliser	14/03/2016 0:7:30 500 8/03/2016 N Split 1 6/04/2015 N split 2	02/11/2015 P_2O_5 60 kg ha^{-1} K_2O 60 kg ha^{-1} 3/3/2016 N split 1 19/04/2016 N split 2
Fungicide	GS25 30/03/2016 GS31/32 19/04/2016 GS49 13/05/2016 GS65 30/05/2016	GS25 29/03/2016 GS31/32 20/04/2016 GS49 16/05/2016 GS65 30/05/2016
Growth regulator	GS30 12/03/2016 GS37 06/04/2016	GS30 20/04/2016 GS37 10/05/2016
Other		3/03/2016 Manganese 1.0 l ha^{-1}

2017

Treatment	Site	
	Teagasc	SRUC
Sowing date	1/10/2016	16/09/2016
Insecticide	7/11/2016 Sumi Aplha 165 ml ha-^{1}	19/10/2016 Hallmark 150 ml ha^{-1}
Herbicide	2/11/2016 Flight 3.0 l ha^{-1} Cropling IPU 1.0 l ha^{-1} 6/04/2017 Croplink Avena 0.3 l ha^{-1} Adigor 1.0 l ha^{-1}	23/09/2016 Picona 3.0 l ha^{-1} 7/04/2017 Ally 15 g ha^{-1}
Fertiliser	10/03/2017 0:7:30 600 kg h^{-1} 10/03/2017 N Split 1 4/04/2017 N split 2	11/11/2016 P_2O_5 60 kg ha^{-1} K_2O 60 kg ha^{-1} 03/03/2017 N split 1 11/04/2017 N split 2
Fungicide	GS25 27/03/2017 GS31/32 10/04/2017 GS49 04/05/2017 GS65 19/05/2017	GS25 06/04/2017 GS31/32 19/04/2017 GS49 05/05/2017 GS65 17/05/17
Growth regulator	GS30 05/04/2017 GS37 20/04/2017	GS30 13/04/2017 GS37 2/05/2017

2018

Treatment	Site	
	Oak Park	Kildalton
Sowing date	2/10/2017	7/10/2017
Herbicide	31/10/2017 Flight 4.0 l ha^{-1}	8/11/2017 Flight 4.0 l ha^{-1}
	9/04/2018 Axial 0.3 l ha^{-1} Adigor 1.0 l ha^{-1}	11/04/2018 Axial 0.3 l ha^{-1} Adigor 1.0 l ha^{-1}
Insecticide	17/11/2018 Sumi Aplha 165 ml ha^{-1}	8/11/2017 Ambush 0.25 l ha^{-1}
Fertiliser	10/03/2018 0:7:30 540 kg ha^{-1}	20/03/2018 Muriate of Potash 230 kg ha^{-1} Sul CAN 240 kg ha^{-1}
	21/03/2018 N split 1	9/04/2018 Sul CAN 352 kg ha^{-1}
	11/04/2018 N split 2	23/04/2018 Sul CAN 148 kg ha^{-1}
Growth regulator	3/04/2018 CeCeCe 750 1 l ha^{-1} Medax Max 0.2 kg ha^{-1}	11/04/2018 CeCeCe 750 1 l ha^{-1} Medax Max 0.2 kg ha^{-1}
	27/04/2018 Medax Max 0.4 kg ha^{-1}	3/05/2018 Medax Max 0.5 kg ha^{-1}
Fungicide	GS25 05/04/2018	GS25 09/04/2018
	GS31/32 19/04/2018	GS31/32 20/04/2018
	GS49 14/05/2018	GS49 17/05/2018
	GS65 23/05/2018	GS65 28/05/2018

Appendix 3 Tables of arcsine transformed data from chapters 2 and 3.

Data from table 2-6. The effect of treatments in SRUC 2015 on the average disease and green leaf area (arcsine transformed) on the top three leaf layers. P Values, LSD's and means were produced from a split-split plot ANOVA analysis

SRUC 2015						
			GS31	GS49	GS65	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	0.136	0.131	0.186	1.257
		1	0.000	0.039	0.054	1.368
		2	0.000	0.036	0.035	1.368
		3	0.050	0.026	0.058	1.362
		4	0.000	0.027	0.020	1.372
	Mean		0.037	0.052	0.070	1.345
High	Volume	unt	0.106	0.110	0.205	1.260
		1	0.000	0.054	0.077	1.364
		2	0.000	0.031	0.049	1.372
		3	0.024	0.041	0.035	1.353
		4	0.000	0.019	0.046	1.348
	Mean		0.026	0.051	0.082	1.339
Standard	Tower	unt	0.131	0.064	0.125	1.340
		1	0.000	0.011	0.060	1.370
		2	0.000	0.032	0.016	1.360
		3	0.037	0.022	0.024	1.331
		4	0.000	0.035	0.027	1.387
	Mean		0.033	0.033	0.050	1.358
Standard	Volume	unt	0.080	0.060	0.130	1.326
		1	0.000	0.029	0.055	1.379
		2	0.000	0.020	0.039	1.368
		3	0.050	0.022	0.014	1.382
		4	0.000	0.016	0.011	1.374
	Mean		0.026	0.029	0.050	1.366

Significance	d.f.	P	LSD	P	LSD	P	LSD	P	LSD
S & N rate (S&N)	1	0.45	0.026	0.01	0.012	0.09	0.034	0.14	0.031
Variety (V)	1	0.06	0.029	0.67	0.013	0.61	0.026	0.9	0.019
Fungicide (F)	4	<.001	0.023	<.001	0.018	<.001	0.033	<.001	0.030
S&N*V	1	0.9	0.032	0.82	0.015	0.59	0.035	0.4	0.030
S&N*F	4	0.13	0.033	0.02	0.025	0.38	0.048	0.07	0.043
V*F	4	0.02	0.038	0.38	0.026	0.86	0.047	0.75	0.041
S&N*V*F	4	0.04	0.050	0.91	0.035	0.91	0.067	0.78	0.059

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Data from table 2-7. The effect of treatments in SRUC 2016 on the average disease and green leaf area (arcsine transformed) on the top three leaf layers. P Values, LSD's and means were produced from a split-split plot ANOVA analysis

SRUC 2016						
			GS31	GS39	GS73	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	0.181	0.131	0.186	1.257
		1	0.000	0.039	0.054	1.368
		2	0.000	0.036	0.035	1.368
		3	0.135	0.026	0.058	1.362
		4	0.000	0.027	0.020	1.372
	Mean		0.063	0.052	0.070	1.345
High	Volume	unt	0.160	0.110	0.205	1.260
		1	0.000	0.054	0.077	1.364
		2	0.000	0.031	0.049	1.372
		3	0.130	0.041	0.035	1.353
		4	0.000	0.019	0.046	1.348
	Mean		0.058	0.051	0.082	1.339
Standard	Tower	unt	0.228	0.064	0.125	1.340
		1	0.000	0.011	0.060	1.370
		2	0.000	0.032	0.016	1.360
		3	0.210	0.022	0.024	1.331
		4	0.000	0.035	0.027	1.387
	Mean		0.088	0.033	0.050	1.358
Standard	Volume	unt	0.168	0.060	0.130	1.326
		1	0.000	0.029	0.055	1.379
		2	0.000	0.020	0.039	1.368
		3	0.139	0.022	0.014	1.382
		4	0.000	0.016	0.011	1.374
	Mean		0.061	0.029	0.050	1.366

Significance	d.f.	P	LSD	P	LSD	P	LSD	P	LSD
S & N rate (S&N)	1	0.15	0.055	0.17	0.010	0.21	0.063	0.41	0.095
Variety (V)	1	0.01	0.026	0.15	0.014	0	0.034	<.001	0.031
Fungicide (F)	4	0.08	0.036	<.001	0.025	<.001	0.040	<.001	0.048
S&N*V	1	0.06	0.051	0.6	0.015	0.81	0.059	0.01	0.089
S&N*F	4	0.67	0.051	0.99	0.032	0.48	0.068	0.23	0.093
V*F	4	0.94	0.035	<.001	0.033	0.04	0.058	0.01	0.066
S&N*V*F	4	0.67	0.059	0.17	0.046	0	0.088	0.28	0.111

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Data from table 2-8. The effect of treatments in SRUC 2017 on the average disease and green leaf area (arcsine transformed) on the top three leaf layers. P Values, LSD's and means were produced from a split-split plot ANOVA analysis

SRUC 2017					
			GS49	GS77	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg GLA
High	Tower	unt	0.168	0.414	0.916
		1	0.077	0.232	1.111
		2	0.136	0.065	1.174
		3	0.155	0.018	1.165
		4	0.129	0.076	1.092
	Mean		0.133	0.161	1.092
High	Volume	unt	0.254	0.522	0.920
		1	0.176	0.351	1.072
		2	0.106	0.136	1.128
		3	0.116	0.072	1.124
		4	0.094	0.031	1.145
	Mean		0.149	0.222	1.078
Standard	Tower	unt	0.113	0.394	0.984
		1	0.116	0.190	1.140
		2	0.100	0.096	1.215
		3	0.139	0.063	1.181
		4	0.139	0.022	1.246
	Mean		0.121	0.153	1.153
Standard	Volume	unt	0.259	0.423	1.007
		1	0.156	0.323	1.105
		2	0.127	0.077	1.146
		3	0.128	0.058	1.177
		4	0.113	0.027	1.211
	Mean		0.157	0.181	1.129

Significance	d.f.	P	LSD	P	LSD	P	LSD
S & N rate (S&N)	1	0.89	0.043	0.16	0.042	0.01	0.025
Variety (V)	1	0.01	0.018	0.03	0.038	0.36	0.047
Fungicide (F)	4	<.001	0.036	<.001	0.031	<.001	0.046
S&N*V	1	0.25	0.040	0.33	0.046	0.8	0.048
S&N*F	4	0.83	0.054	0.19	0.049	0.32	0.061
V*F	4	<.001	0.048	<.001	0.051	0.49	0.071
S&N*V*F	4	0.46	0.072	0.12	0.069	0.68	0.092

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Data from table 2-9. The effect of treatments in Teagasc 2015 on the average disease and green leaf area (arcsine transformed) on the top three leaf layers. P Values, LSD's and means were produced from a split-split plot ANOVA analysis

			Teagasc 2015			
			GS31	GS49	GS65	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	0.123	0.206	0.177	0.993
		1	0.000	0.101	0.074	1.298
		2	0.000	0.000	0.052	1.272
		3	0.030	0.080	0.030	1.264
		4	0.000	0.000	0.011	1.318
	Mean		0.031	0.078	0.069	1.229
High	Volume	unt	0.144	0.189	0.247	0.982
		1	0.000	0.099	0.114	1.189
		2	0.000	0.000	0.072	1.314
		3	0.055	0.080	0.061	1.295
		4	0.000	0.000	0.065	1.297
	Mean		0.040	0.074	0.112	1.215
Standard	Tower	unt	0.078	0.198	0.155	1.012
		1	0.000	0.071	0.092	1.160
		2	0.000	0.000	0.058	1.191
		3	0.048	0.059	0.043	1.292
		4	0.000	0.000	0.042	1.343
	Mean		0.025	0.066	0.078	1.199
Standard	Volume	unt	0.135	0.237	0.188	1.013
		1	0.000	0.095	0.102	1.181
		2	0.000	0.000	0.053	1.243
		3	0.035	0.085	0.071	1.269
		4	0.000	0.000	0.066	1.259
	Mean		0.034	0.083	0.096	1.193

Significance	d.f.	P	LSD	P	LSD	P	LSD	P	LSD
S & N rate (S&N)	1	0.24	0.042	0.93	0.068	0.85	0.050	0.56	0.128
Variety (V)	1	0.06	0.021	0.51	0.040	0.01	0.017	0.51	0.035
Fungicide (F)	4	<.001	0.012	<.001	0.034	<.001	0.027	<.001	0.056
S&N*V	1	0.95	0.039	0.32	0.065	0.13	0.046	0.81	0.122
S&N*F	4	0.08	0.039	0.52	0.065	0.25	0.050	0.26	0.121
V*F	4	0.03	0.023	1	0.052	0.56	0.037	0.4	0.076
S&N*V*F	4	0.02	0.040	0.86	0.080	0.98	0.061	0.44	0.138

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Data from table 2-10. The effect of treatments in Teagasc 2016 on the average disease and green leaf area (arcsine transformed) on the top three leaf layers. P Values, LSD's and means were produced from a split-split plot ANOVA analysis

Teagasc 2016						
			GS31	GS49	GS75	
S & N rate	Variety	Fungicide	Avg dis	Avg dis	Avg dis	Avg GLA
High	Tower	unt	0.224	0.173	0.599	0.000
		1	0.000	0.102	0.610	0.358
		2	0.000	0.105	0.604	0.494
		3	0.205	0.077	0.535	0.461
		4	0.000	0.088	0.346	0.702
	Mean		0.086	0.109	0.539	0.403
High	Volume	unt	0.235	0.212	0.584	0.165
		1	0.000	0.107	0.521	0.338
		2	0.000	0.112	0.536	0.481
		3	0.199	0.099	0.592	0.501
		4	0.000	0.092	0.426	0.663
	Mean		0.087	0.124	0.532	0.430
Standard	Tower	unt	0.222	0.211	0.607	0.304
		1	0.000	0.095	0.556	0.363
		2	0.000	0.098	0.527	0.420
		3	0.188	0.092	0.599	0.503
		4	0.000	0.093	0.331	0.837
	Mean		0.082	0.118	0.524	0.485
Standard	Volume	unt	0.211	0.193	0.580	0.402
		1	0.000	0.088	0.635	0.390
		2	0.000	0.103	0.492	0.560
		3	0.166	0.084	0.527	0.499
		4	0.000	0.104	0.319	0.799
	Mean		0.075	0.114	0.511	0.530

Significance	d.f.	P	LSD	P	LSD	P	LSD	P	LSD
S & N rate (S&N)	1	0.15	0.037	0.17	0.032	0.21	0.051	0.41	0.007
Variety (V)	1	0.01	0.019	0.15	0.016	0	0.034	<.001	0.032
Fungicide (F)	4	0.08	0.019	<.001	0.014	<.001	0.076	<.001	0.047
S&N*V	1	0.06	0.035	0.6	0.030	0.81	0.050	0.01	0.032
S&N*F	4	0.67	0.034	0.99	0.030	0.48	0.101	0.23	0.059
V*F	4	0.94	0.022	<.001	0.022	0.04	0.100	0.01	0.065
S&N*V*F	4	0.67	0.037	0.17	0.036	0	0.142	0.28	0.087

Avg dis = Average disease, Avg GLA = Average green leaf area Unt = untreated, 1 = 1 spray, 2 = 2 spray, 3 = 3 spray, 4 = 4 spray. The residual d.f. are 3, 6 and 48 for the main plot, sub-plot and sub- plot strata respectively.

Data from table 2-11. The effect of treatments in Teagasc 2017 on the average disease and green leaf area (arcsine transformed) on the top three leaf layers. P Values, LSD's and means were produced from a split-split plot ANOVA analysis

Teagasc 2017						
			GS31		GS49	
S & N rate	Variety	Fungicide	Avg dis		Avg dis	
High	Tower	unt	0.519		0.227	
		1	0.505		0.583	
		2	0.310		0.821	
		3	0.308		0.859	
		4	0.076		1.180	
	Mean		0.344		0.734	
High	Volume	unt	0.609		0.523	
		1	0.462		0.749	
		2	0.224		1.054	
		3	0.178		1.121	
		4	0.088		1.245	
	Mean		0.312		0.938	
Standard	Tower	unt	0.519		0.630	
		1	0.437		0.581	
		2	0.307		0.809	
		3	0.294		0.863	
		4	0.033		1.360	
	Mean		0.318		0.849	
Standard	Volume	unt	0.450		0.845	
		1	0.360		0.906	
		2	0.210		1.101	
		3	0.162		1.085	
		4	0.051		1.352	
	Mean		0.247		1.058	
Significance		d.f.	P	LSD	P	LSD
S & N rate (S&N)		1	0.13	0.070	0.09	0.154
Variety (V)		1	0.05	0.053	0	0.112
Fungicide (F)		4	<.001	0.048	<.001	0.077
S&N*V		1	0.39	0.071	0.96	0.155
S&N*F		4	0.36	0.077	<.001	0.150
V*F		4	0.01	0.075	0.02	0.138
S&N*V*F		4	0.4	0.106	0.47	0.196

Data from table 2-12. The effect of GS65 timing on the Fusarium infection (arcsine transformed) occurred at Teagasc 2016 & 2017. P Values, LSD's and means were produced from a split-split plot ANOVA analysis. "+" treatments are the 4 spray programme, "-" treatments are a combination of untreated, 1, 2 and 3 spray programmes.

S & N rate	Variety	Head spray	Teagasc 2016	Teagasc 2017
High	Tower	+	0.258	0.156
High	Tower	-	0.324	0.197
	Mean		0.291	0.177
High	Volume	+	0.356	0.142
High	Volume	-	0.478	0.202
	Mean		0.417	0.172
Standard	Tower	+	0.209	0.112
Standard	Tower	-	0.304	0.209
	Mean		0.256	0.160
Standard	Volume	+	0.243	0.147
Standard	Volume	-	0.424	0.223
	Mean		0.333	0.185

Significance		P	LSD	P	LSD
S & N rate (S&N)	1	0.02	0.03	0.15	0.1
Variety (V)	1	<.001	0.05	0.31	0.14
Fungicide (F)	4	<.001	0.08	<.001	0.12
S&N*V	1	0.25	0.05	0.36	0.17
S&N*F	4	0.22	0.13	0.21	0.23
V*F	4	0.06	0.15	0.97	0.28
S&N*V*F	4	0.66	0.27	0.47	0.5

Data from table 2-28. The effects of treatments on average disease and GLA (arcsine transformed) for the top three leaf layers for Kildalton (KIL) and Oak Park (OP). P Values, LSD's and means were produced from a split-split plot ANOVA analysis.

		Avg Dis L1 & L2		Avg GLA L1 & L2	
Variety	**Fungicide**	OP	KIL	OP	KIL
Cassia	**2 spray**	0.555	0.621	0.568	0.345
Cassia	**3 spray**	0.391	0.592	0.859	0.377
Cassia	**4 spray**	0.143	0.081	1.164	0.809
Cassia	**3 spray + CTL**	0.103	0.077	1.175	0.773
Cassia	**4 spray + CTL**	0.103	0.050	1.166	0.842
Cassia	**4 spray + proline**	0.098	0.063	1.213	0.775
	mean	**0.232**	**0.248**	**1.024**	**0.654**
Kosmos	**2 spray**	0.382	0.733	0.959	0.410
Kosmos	**3 spray**	0.426	0.644	0.918	0.492
Kosmos	**4 spray**	0.219	0.100	1.210	0.968
Kosmos	**3 spray + CTL**	0.121	0.130	1.341	0.916
Kosmos	**4 spray + CTL**	0.125	0.125	1.341	0.975
Kosmos	**4 spray + proline**	0.117	0.127	1.318	1.000
	mean	**0.232**	**0.310**	**1.181**	**0.794**
Tower	**2 spray**	0.658	0.633	0.394	0.289
Tower	**3 spray**	0.441	0.497	0.690	0.452
Tower	**4 spray**	0.302	0.085	0.944	0.908
Tower	**3 spray + CTL**	0.128	0.072	1.079	0.965
Tower	**4 spray + CTL**	0.124	0.070	1.177	0.890
Tower	**4 spray + proline**	0.119	0.134	1.114	0.881
	mean	**0.295**	**0.249**	**0.900**	**0.731**
Volume	**2 spray**	0.658	0.701	0.431	0.320
Volume	**3 spray**	0.474	0.415	0.718	0.516
Volume	**4 spray**	0.196	0.103	1.150	0.863
Volume	**3 spray + CTL**	0.161	0.102	1.199	0.865
Volume	**4 spray + CTL**	0.138	0.056	1.247	0.834
Volume	**4 spray + proline**	0.128	0.079	1.120	0.914
	mean	**0.292**	**0.243**	**0.978**	**0.719**

Significance	**df**	P	LSD	P	LSD	P	LSD	P	LSD
Variety (V)	**3**	0.012	0.199	0.024	0.201	0.001	1.086	0.092	ns
Fungicide (F)	**5**	<.001	0.424	<.001	0.237	<.001	1.035	<.001	0.704
V x F	15	0.139	ns	0.067	ns	0.191	ns	0.856	ns

[1] Average area infected by disease for leaf 1 and leaf 2. [2] Average green leaf area for leaf 1 and leaf 2. Ns = not significant (p>0.05). The residual d.f were 9 and 60 for the main plot and sub-plot respectively

Data from table 3-2. Effects of variety and fungicide on the total severity (arcsine transformed) of all disease averaged over the top three leave for GS31, GS39 and GS55 while GS55+2 was top two leaves. Means an P- values from values produced by ANOVA analysis

2016

Variety	Fungicide	GS31		GS39		GS55		GS55+2 weeks	
Tower	**Untreated**	0.085		0.162		0.237		0.472	
Tower	**4 spray**	0.039		0.109		0.122		0.190	
Volume	**Untreated**	0.051		0.156		0.240		0.538	
Volume	**4 spray**	0.047		0.148		0.133		0.187	
Variety mean	**Tower**	0.062		0.135		0.179		0.331	
	Volume	0.049		0.152		0.187		0.363	
Fungicide mean	**Untreated**	0.043		0.128		0.127		0.505	
	4 spray	0.068		0.159		0.239		0.189	
Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.149	ns	0.602	ns	0.636	ns	0.367	ns
Fungicide (F)	**1**	0.006	0.015	0.129	ns	<.001	0.033	0.007	0.164
V*F	**1**	0.013	0.022	0.254	ns	0.76	ns	0.688	ns

2017

Variety	Fungicide	GS31		GS39		GS55		GS55+2 weeks	
Tower	**untreated**	2.059		0.395		1.967		24.360	
Tower	**4 spray**	2.570		0.846		0.096		0.650	
Volume	**untreated**	1.604		0.256		3.097		24.340	
Volume	**4 spray**	2.796		0.815		0.284		0.880	
Variety mean	**Tower**	2.31		0.62		1.03		12.51	
	Volume	2.20		0.54		1.69		12.61	
Fungicide mean	**untreated**	1.83		0.33		0.19		24.35	
	4 spray	2.68		0.83		2.53		0.77	
Significance	**df**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**	**P**	**LSD**
Variety (V)	**1**	0.847	ns	0.291	ns	0.095	ns	0.741	ns
Fungicide (F)	**1**	0.256	ns	<.001	0.012	<.001	0.035	<.001	0.057
V*F	**1**	0.628	ns	0.313	ns	0.643	ns	0.737	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Data from table 3-4. The effect of variety and fungicide on the amount WSC concentration (conc.) at anthesis (arcsine transformed). Means, P and LSD values presented were produced by ANOVA analysis on arcsine transformed data.

		WSC conc. % at anthesis			
Variety	**Fungicide**	**2016**		**2017**	
Tower	4 spray	0.40		0.36	
Tower	Untreated	0.37		0.37	
Volume	4 spray	0.33		0.36	
Volume	Untreated	0.32		0.37	
Variety mean	Tower	0.39		0.36	
	Volume	0.35		0.36	
Fungicide mean	4 spray	0.36		0.36	
	Untreated	0.35		0.37	
Significance	df	P	LSD	P	LSD
Variety (V)	1	0.068	ns	0.87	ns
Fungicide (F)	1	0.085	ns	0.758	ns
V*F	1	0.652	ns	0.869	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Data from table 3-5. The effects treatments on % water-soluble carbohydrate (WSC) utilisation. Means, P-values and LSD's presented from values produced by ANOVA analysis on arcsine transformed data

		% WSC Utilisation			
Variety	**Fungicide**	**2016**		**2017**	
Tower	**Treated**	1.14		1.27	
Tower	**untreated**	1.26		1.39	
Volume	**Treated**	1.23		1.29	
Volume	**untreated**	1.29		1.38	
Variety Mean	**Tower**	1.20		1.33	
	Volume	1.26		1.34	
Treatment mean	**Control**	1.19		1.28	
	Treated	1.28		1.39	
Significance	**df**	P	LSD	P	LSD
Variety (V)	**1**	0.197	ns	0.944	ns
Fungicide (F)	**1**	0.003	0.047	0.012	0.078
V*F	**1**	0.2	ns	0.66	ns

The residual d.f were 3 and 6 for the main plot and sub-plot respectively

Data from table 3-7 and 3-8. The effects of fungicide treatment and post-anthesis manipulations and water-soluble carbohydrates (WSC) utilisation. Means, P values and LSD produced from ANOVA analysis on arcsine transformed data.

			RO		De-grain	
Variety	**Fungicide**	**Manipulation**	**2016**	**2017**	**2016**	**2017**
Tower	**4 spray**	**Control**	1.31	1.30	1.33	1.30
Tower	**4 spray**	**De-grain**	1.18	1.13	1.09	0.85
Tower	**Untreated**	**Control**	1.33	1.32	1.31	1.32
Tower	**Untreated**	**De-grain**	1.33	1.30	1.28	1.30
Volume	**4 spray**	**Control**	1.36	1.31	1.38	1.32
Volume	**4 spray**	**De-grain**	1.26	1.16	0.97	0.87
Volume	**Untreated**	**Control**	1.35	1.30	1.33	1.29
Volume	**Untreated**	**De-grain**	1.28	1.27	1.10	1.22
Variety Mean	**Tower**		1.29	1.26	1.25	1.19
	Volume		1.31	1.26	1.20	1.17
Fungicide mean	**4 spray**		1.28	1.22	1.19	1.08
	Untreated		1.32	1.30	1.25	1.28
Manipulation mean	**Control**		1.34	1.31	1.34	1.31
	De-grain		1.26	1.22	1.11	1.06

Significance	**df**	P	LSD	P	LSD	P	LSD	P	LSD
Variety (V)	**1**	0.64	ns	0.94	ns	0.22	ns	0.52	ns
Fungicide (F)	**1**	0.29	ns	0.01	0.05	0.16	ns	0	0.1
Manipulation (M)	**1**	0.01	0.05	<.001	0.03	<.001	0.06	<.001	0.05
V*F	**1**	0.3	ns	0.3	ns	0.59	ns	0.38	ns
V*M	**1**	0.6	ns	0.67	ns	0	0.11	0.65	ns
F*M	**1**	0.11	ns	<.001	0.06	0	0.1	<.001	0.1
V*F*M	**1**	0.3	ns	0.68	ns	0.7	ns	0.69	ns

The residual d.f were 3, 6 and 12 for the main plot, sub-plot and sub-sub plot respectively