IDENTIFYING AND EVALUATING COMPETITIVE TRAITS IN WHEAT FOR SUSTAINABLE WEED MANAGEMENT

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Abstract

The management of weed species *Alopecurus myosuroides* (black-grass) in arable agriculture is largely achieved through use of herbicides. However, resistant populations are increasingly commonplace and new modes of action are proving elusive. Growers use integrated weed management (IWM) strategies to manage the weed seedbank, such as rotational ploughing to bury seed and delayed drilling to reduce weed numbers within a crop. Competitive cultivars may contribute to IWM, but testing cultivars is a long, expensive process.

The aims of this studentship were to identify the traits that confer enhanced crop competitive ability and determine if these can be used to predict competitive ability of new cultivars. This was investigated on outdoor sand-beds and in field trials. Commercial wheat cultivars were grown alongside *A. myosuroides.* Various wheat traits were measured throughout growth. The seed return of *A. myosuroides* was quantified at maturity, and yield was harvested in the field. Pearson's correlations and multivariate analysis were used to identify traits related to competition, and Linear Mixed Models (LMM) were used to identify predictive traits. Two models of crop-weed interactions were parameterised for the cultivars. Potential interactions between cultivar choice and other IWM strategies (delayed sowing and increased sowing rate) was assessed experimentally and through simulation models.

Cultivar differences in suppressive ability were most evident between the extreme ends. Various traits were related to a cultivar's ability to suppress *A. myosuroides* seed return, such as early height and tillering parameters, though no traits were consistent across all experiments. Few traits could be related to tolerance to yield loss. Suppressive ability can be ascertained

early in the growing season, but the relationship with individual traits can change direction, possibly depending on the availability of belowground resources. Generally, earlier maturity and a conserved tillering strategy appears to be more suppressive. Cultivar choice is largely compatible with delayed sowing and increased sowing date. The effect of environmental variability on relationships between traits and competitive ability requires further investigation before they can be employed as predictors, particularly in the context of belowground competition.

Publications

Peer-reviewed publications

ANDREW IKS, STORKEY J and SPARKES D (2015) A review of the potential of competitive cereal cultivars as a tool in integrated weed management. *Weed Research* 55, 239-248.

Presentations and papers in symposia

ANDREW IKS, STORKEY J and SPARKES D (2014) Identifying the traits in cereals that confer greater suppressive ability against *Alopecurus myosuroides*. *Aspects of Applied Biology*, 127:135-140.

ANDREW IKS and STORKEY J (2014) Is there a future for predicting the competitive ability of cultivars? A case study of wheat in the UK. *Proceedings of WSSA-CSWS symposium*, Vancouver Feb 2014.

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Abbreviations

a – Percentage yield loss as weed density → ∞

ABGW – Early aboveground weight (g)

DAS – Days after sowing

GAI – Green area index; the ratio of green tissue area to ground area

GAI_W – Weed green area index; used in the calculation of Gw at canopy closure

G_W – Relative weed green area

i – Yield loss per weed per m^2 as density of the weed population approach zero

L_0 – Seedling green area at zero thermal time / initial green area (cm^2)

LAI_C – Crop leaf area index; used in the calculation of L_W at canopy closure (cm^2)

LAI_W – Weed leaf area index; used in the calculation of LW at canopy closure (cm^2)

LAR – Leaf area ratio; the ratio of leaf area to total plant biomass

LMM – Linear mixed model; a linear predictor model that includes random and fixed effects

L_W – Relative weed leaf area ratio

LWR – Leaf weight ratio; a ratio of total weight allocated to leaves

m – Maximum yield loss in a given scenario

NAR – Net assimilation rate; an indirect measure of net carbon gain ($gm^{-2}\ d^{-1}$)

ptt – Photothermal time; unite description of time, accounting for accumulated day degrees and photoperiod over a defined period

q – Relative damage coefficient; yield loss per unit leaf area at low weed densities

RDA – Redundancy analysis; a multivariate analysis tool

RGR_{GA} – Green area relative growth rate; the rate of green area growth per unit area per day ($cm^2\ cm^{-2}\ tt^{-1}$)

RGR_W – Total dry weight relative growth rate; the rate of biomass growth per unit mass per day ($g\ g^{-1}\ tt^{-1}$)

RWR – Root weight ratio; the ratio of root weight to aboveground weight

SLA – Specific leaf area; a measure of leaf thinness ($m^2\ g^{-1}$)

SSA – Specific stem area; a measure of stem photosynthetic area ($m^2\ g^{-1}$)

TGW – Thousand grain weight (g)

tt – Thermal time; unit description of time, accounting for accumulated day degrees over a defined period

UK – United Kingdom

W_0 – Seedling weight at zero thermal time

YL – Percentage yield loss

Logistic functions of height

c – Upper asymptote of height

m – Point of inflexion; the time of maximum growth rate

a – Initial height

Table of Contents

List of tables

List of Figures

1 Introduction

1.1 Plant competition and arable agriculture

1.1.1 Defining plant competition

Competition can be defined as an interaction that takes place between individuals or groups of organisms (most commonly species), where the fitness of one group or individual is detrimentally impacted by the presence of another. For it to occur, the two competing individuals or groups must share one or more resources with limited availability (Zimdahl, 2004).

There have been many efforts to define, isolate and measure competition in a manner especially relevant to plants, which lead to disagreements in the literature (Grace & Tilman, 1990). Some have indicated that various facets of competition are excluded from simpler definitions, such as "direct interference and indirect exploitation of shared resources", within which multiple types of competition may occur (Connell, 1990). Nonetheless, even Connell (1990) acknowledges that the definition can be simplified to "a reciprocal negative interaction between two organisms".

1.1.2 Competition in the agricultural system

In the agricultural system, there is careful management between producing the highest yield achievable whilst minimising costs. Any undesirable plant (weed) in this system can reduce profits through decreasing yield quality or quantity, or through the cost of control efforts. They may be hosts for disease or be toxic to grazers in grassland, or undermine the structure of buildings. Weeds have been reported as the most importance pest problem in wheat (*Triticum aestivum* L.)

agriculture, able to inflict a 34% potential yield loss on the crop globally (Oerke, 2006).

Agricultural systems differ from natural systems in a number of ways. For cereal production the ground is prepared so that mass germination occurs at once, manufactured to favour the monoculture of choice, causing it to resemble an early successional environment. This favours ruderal species, which are typified by high growth rates to allow them to grab resources but tend to suffer competitive exclusion as succession proceeds (Grime, 2001). Nutrients that are often limiting in the soil are available in high quantities due to industrial fertiliser inputs, which tend to reduce the importance of belowground competition in these systems (Lamb *et al.*, 2007; Wang *et al.*, 2010).

1.1.3 Herbicides and weed management in the UK

Pests can pose a substantial risk to profitable yield. Of all pests, weeds have the potential to incur the greatest yield loss, through competition with the crop and decreasing yield quality (Oerke, 2006). The introduction of herbicides allowed very effective and relatively cheap control of weed species, relieving arable farmers of a heavy financial burden and contributing to the increase in average yield seen during the period of their adoption (Ceccarelli, 1996; Moss *et al.*, 2004). The methods of weed control employed prior to herbicides fell into disfavour, though continued to play a pivotal role in organic agriculture.

Unfortunately, the over-reliance on chemical control has led to a number of environmental and agronomic concerns. Herbicides can damage non-target species which support the arable ecosystem. They are water-soluble and able to enter surface waters. This threatens non-target aquatic plant species,

disturbing lake and river ecosystems. Herbicide resistance is now widespread amongst many problematic weed species (Heap, 1997; Moss *et al.*, 2011). Resistance can occur in the form of enhanced metabolism and resistance to inhibitors, and develops as part of a process of natural selection. Regular herbicide applications increase the fitness of individuals with herbicide resistance, causing the trait to increase proportionally through the population.

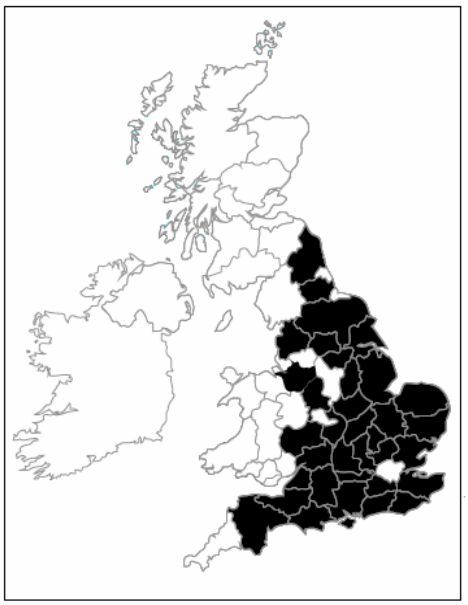

Figure 1.1 - The distribution of reported herbicide resistance in *A. myosurodes* in the UK from Moss *et al.*, (2011)

In addition to resistance concerns, EU regulations are reducing the number of herbicide options and new modes of action are proving elusive, further increasing the risk of the development of resistance to the remaining products (Duke, 2012). Finally, the application of herbicides (combined with other changes in farmland management) is leading to the reduction in arable plant diversity and having wider impacts on farmland biodiversity and ecosystem function (Moonen & Bàrberi, 2008; Storkey *et al.*, 2012).

1.1.4 Non-chemical weed control

In response to these challenges there is interest in the potential for integrating non-chemical (or 'cultural') control options into weed control strategies. An increasing number of studies regarding non-chemical weed control have been published over the past two decades (Harker & O'Donovan, 2013; Lutman *et al.*, 2013). A combination of approaches, often termed Integrated Weed Management (IWM), have been employed increasingly in the UK to compensate for loss of herbicide efficacy, and have been recognised to contribute to reducing the weed seed-bank. Many cultural tools require financial or temporal investments, so are unpopular options when compared to herbicides. Cultural control methods vary in effectiveness from year to year, whereas herbicides are more reliable (Bastiaans *et al.,* 2008). As such, they are primarily used by the organic sector, or when herbicide-resistant populations are established on a farm (Bond & Grundy, 2001).

Cultural control techniques include crop rotation, which reduces build-up of crop-specific problem weeds by introducing a variable environment with more competitive break crops (Liebman & Davis, 2000; Bond & Grundy, 2001). Drilling autumn-sown crops late also limits weed establishment as there is less time from ground preparation for germination before temperatures become unfavourable (Kolbe, 1980; Cosser *et al.,* 1997). This technique can be combined with a stale seedbed, to encourage germination of weeds and destroying them before the crop is planted (Riemens *et al.,* 2007). Cover crops, intercrops and mulches can also decrease light available to weeds, as well as have some allelopathic effects (Liebman & Davis, 2000; Bond & Grundy, 2001). Higher seed rate increases the early biomass of crop, which increases the quantity of light

that the stand intercepts, making it difficult for weeds to develop during the early phases (O'Donovan *et al.,* 2000, Mennan & Zandstra, 2005). Mechanical weed removal is still used, but primarily in organic agriculture (Bond & Grundy, 2001). Pre-germination techniques including ploughing to bury seed into the soil profile where it is unlikely to germinate. It is considered specifically important in managing weeds whose seeds only have a short dormancy (such as *Anisantha sterilis* and *A. myosuroides*) (Moss & Clarke, 2008). However, if a field is ploughed too frequently viable seed with greater capacity for dormancy will return to the surface.

Finally, farmers have the option of using more competitive crop cultivars (often terms 'varieties') to suppress weed populations. The use of competitive cultivars and the interactions with other cultural control options will be addressed in this thesis.

1.1.5 Study species *Alopecurus myosuroides*

The model weed for the suppression studies was *Alopecurus myosuroides* (Huds.), common name black-grass. It is an annual grass weed that germinates mainly in September and early October (although there is a smaller flush in the spring) and a seed decline rate of 80% per year. It was chosen as it is a well-studied species that causes significant yield losses in winter-sown cereal crops in (Moss, 1987) with widespread resistance to many herbicides in many North-Western European countries (Lutman *et al.,* 2013; Moss *et al.*, 2011; Keshtkar *et al.*, 2015). Development of resistance in *A. myosuroides* has been amplified by the dependence upon herbicides alone. However, there is renewed interest in non-chemical weed control for this species (Lutman *et al.,* 2013). The use of competitive cultivars is one such potential tool.

1.2 Competitive crop cultivars

Competitive cultivars could reduce the seed return of a weed species and contribute to IWM strategies, in turn reducing the pressure on herbicides and improving the sustainability of cropping systems. For example, in Greece, the use of competitive cultivars alone was demonstrated to allow for a 50% reduction in recommended levels of herbicides in wheat (Travlos, 2012). Cultivars could reduce the fitness of a weed population through competition for limited resources (Christensen, 1995) and production of chemical exudates that reduce growth (Wu *et al.,* 1999). This results in decreased weed seed return and, consequently, decrease its population. Particular cultivars may reduce the economic burden of weeds by resisting yield loss (Reeves & Brooke, 1977; Vandeleur & Gill, 2004). They are a potentially attractive option because they do not incur any inherent additional costs – rather, the ability to control weeds or resist yield loss is a characteristic of the crop itself.

Studies on the comparative competitive ability of cultivars has received increasing interest in all manner of crop species. Winter-sown cereals are the focus of this thesis.

1.2.1 Competitive cereal cultivars

Work in the 1970s demonstrated differences in competitive ability between winter wheat cultivars. At this early stage, work was focused on the ability of different cultivars to resist yield losses. Four winter wheat cultivars were compared for their ability to withstand competitive pressure, with a range of 28 – 39% reduction in yield when *Lolium multiflorum* (Lam.) was present at c.100 plants m^{-2} (Appleby *et al.,* 1976). Differences between cultivars were also shown between 29 cultivars in competition with *Lolium rigidum* (Gaudin), where, at densities

of 1,500 weeds m^{-2}, yield reductions ranged from 23.1% to 47.8% (Reeves & Brooke, 1977).

Later, variation in their capacity to decrease weed fitness generated research interest. For example, two cultivars of wheat and barley (*Hordeum vulgare* L.) showed different capacities to reduce the number of seed heads produced by *A. myosuroides* (Moss, 1985). Wicks *et al.* (1986) demonstrated that winter wheat cultivars differed in their ability to negatively impact on the establishment and growth of the summer annuals *Amaranthus retroflexus* (L.), *Portulaca oleracea* (L.), *Echinocholoa crus-galli* (L.) and *Eragrostis cilianensis* (All.). In this study, control of weeds ranged from 59% to 96% when compared to plots where the crop had been removed by cultivation prior to May.

Comparative studies of this type are, however, of limited value outside of the experimental pool of cultivars. It is important that more predictive approaches are developed that can be used to assess new cultivars or guide future crop breeding efforts. With this in mind, this review discusses the distinction between two modes of competitive ability, and assesses what is known about the traits that determine the competitive ability of cultivars. Allelopathy has more recently started to attract interest in cereals and may be of importance in determining competitive outcomes (Bertholdsson, 2005) but is not considered here in detail. For a recent review of allelopathy in cereal crops summarises current research, see Worthington and Reberg-Horton (2013).

1.3 **Suppression of weeds versus tolerance of weeds**

Suppressive ability is defined as the capacity of one species to reduce the fitness of another through resource acquisition.

Tolerance ability is the capacity of one species to maintain fitness in the presence of another species. (Goldberg, 1990; Grace, 1990). These have been referred to by different terms in the literature (Watson *et al.,* 2006; Wang *et al.,* 2010), but here will be described as suppressive ability and tolerance ability (Hansen *et al.,* 2008).

There is value in defining suppression and tolerance, as both have different outcomes in terms of weed management. In crop – weed competition scenarios, suppressive ability is the ability of the crop to restrict the growth and seed production of undesirable species. Tolerance ability is used to refer to the crop's ability to withstand the competitive impact of neighbours and resist yield loss (Kirkland & Hunter, 1991; Cosser *et al.,* 1997). However, it does not necessarily imply any control is exerted on a weed population. If strong tolerator / weak suppressor cultivars were to be employed long-term, weed populations may reach levels that can no longer be tolerated (Appleby *et al.,* 1976; Jordan, 1993; Lemerle *et al.,* 1996).

Variation in suppressive ability between cultivars of wheat have been observed against *Lolium rigidum* (Gaud.) (Lemerle *et al.*, 1996), *Aegilops cylindrica* (Host) (Ogg & Seefeldt, 1999), *Galium aparine* (L.) (Mennan & Zandstra, 2005), and weed mixtures (Wicks *et al.*, 1986; Cosser *et al.,* 1997, Korres & Froud-Williams, 2002).

Differences in tolerance ability have been identified between cultivars of wheat (Appleby *et al.,* 1976; Reeves & Brooke, 1977; Challaiah *et al.,* 1986; Vandeleur & Gill, 2004; Zerner *et al.,* 2008). Tolerance has been observed to vary little between winter wheat cultivars in comparison to suppressive ability and is often inconsistent over seasons and locations (Jordan, 1993;

Cousens & Mokhtari, 1998; Olesen *et al.,* 2004; Benaragama *et al.,* 2014). This has led to the suggestion that competitive tolerance does not exist as a mechanism to resist the suppressive effects of a neighbour sharing finite resources. So-called 'tolerance' traits may instead be stress-resistance traits (Wang *et al.,* 2010).

Since the distinction between suppression and tolerance has been made, research has sought to establish if they are correlated. Negative relationships between tolerance and suppressive ability have been reported; (Miller & Werner, 1987); positive relationships in other cases; (Goldberg & Fleetwood, 1987, Watson *et al.,* 2006); or no perceivable relationship at all (Goldberg & Landa, 1991; Cahill *et al.*, 2005). Older cultivars tend to be better suppressors and tolerators than modern cultivars (Vandeleur & Gill, 2004). Traits have typically been defined as having either suppressive or tolerance qualities (see section 1.4). Although some have been suggested to confer both, such as wheat height in Seefeldt *et al*. (1999), there is no clear consensus on how they are linked.

Suppressive ability and tolerance are best considered as separate entities due to the uncertainty of the relationship between them and, where possible, this distinction is made throughout this thesis. To describe a trait broadly as conferring a 'competitive advantage' could be misleading, as it may suggest that it confers both suppressive and tolerance ability (Lemerle *et al.,* 2001; Cahill *et al.,* 2005). When used in this thesis, 'competitive ability' will refer to both suppressive ability and tolerance as both are quantified experimentally but the one the data are relevant to will also be made clear.

1.4 The role of traits in competitive ability

1.4.1 Defining a trait

Since the advent of evolutionary theory, research has sought to understand what features give one species a competitive advantage over another. In plant ecology, work indicates what suites of plant traits confer benefits to particular ecological strategies. The term 'trait' indicates a plant characteristic which may be used as a predictor of fitness in different environments. Some confusion has surrounded the use of this term. There are attempts to split definitions into levels of organisation, with the term 'trait' being reserved for any feature that is morphological, physiological or phenological and can be identified and measured at the level of the individual (Violle *et al.,* 2007). This thesis will adhere to this definition where feasible, though target traits in some research do not match the criteria and, indeed, suppressive ability itself is often referred to as a trait (Wang *et al.*, 2010).

1.4.2 Height

Early interest in competitive cultivar traits mainly focussed on maximum canopy height. This originated from the observed differences between the 'new' semi-dwarf and 'old' (taller) cultivars of wheat. Whilst lower yielding in weed-free situations, taller cultivars were typically better tolerators of weed pressure and suppressors of weed growth (Appleby *et al.,* 1976; Lemerle *et al.,* 1996; Ogg & Seefeldt, 1999; Vandeleur & Gill, 2004). The benefit of height has been demonstrated in wheat in competition with *Bromus tectorum* (L.) (Challaiah *et al.,* 1986), *A. cylindrica* (Ogg & Seefeldt, 1999), and oats (*Avena sativa* L.), barley and wheat against *G. aparine* (Brain *et al.,* 1999).

However, height cannot alone explain variation in competitive ability. Wicks *et al*. (2004) compared thirteen red winter wheat cultivars in their ability to suppress a mixture of annual weeds. Two of the shortest cultivars exhibited stronger suppressive abilities than many tall cultivars. This was an indication that competitive ability cannot be attributed to a single trait, as has since been acknowledged by many authors (Moss, 1985; Lemerle *et al.*, 1996; Roberts *et al.*, 2001; Mennan & Zandstra, 2005; Watson *et al.*, 2006). The relative contribution of height to suppression and tolerance has often been linked to the ability to intercept photosynthetically active radiation (PAR) (Wicks *et al.*, 1986; Gooding *et al.*, 1993; Lemerle *et al.*, 1996), but a strong relationship between heights and PAR interception has not always been found (Blackshaw, 1994). The relative importance of height may be also related to weed species. *Veronica hederifolia*, a shade tolerant species, achieved highest biomass under the tall Maris Widgeon compared to shorter cultivars, and the authors suggested that the species benefits from shade during establishment (Gooding *et al.*, 1993). A range of other traits, reviewed below, have also been associated with weed suppression or tolerance in cereal cultivars.

1.4.3 Early vigour

Certain plant strategies are more successful than others under particular environmental pressures (Grime, 1977; Grime, 1979). The arable farming environment selects for ruderal traits, including rapid emergence (Didon, 2002) and high biomass accumulation early in the establishment phase (Grime, 2001) - both adaptations to fertile environments with high disturbance. Early vigour of a cultivar is related to crop establishment and the rate at which aboveground material is produced, and has been correlated to morphological leaf traits

such as leaf area in the earliest phases of growth (Rebetzke & Richards, 1999). Traits relating to leaf size, specific leaf area and rate of production vary between cultivars, and have been linked to higher suppressive ability (Huel & Hucl, 1996; Coleman *et al.*, 2001; Rebetzke *et al.*, 2004; Vandeleur & Gill, 2004; Zerner *et al.*, 2008).

Other indicator traits of early vigour, including early crop height, cover and biomass, are potentially useful for assessing variation in suppressive ability (Lemerle *et al.*, 1996; Olesen *et al.*, 2004; Worthington *et al.*, 2013) and could be valuable for designing screening protocols (see below). Bertholdsson (2005, 2011) used early crop mass as an indicator of vigour in wheat and barley, and found it to be one of two traits (along with allelopathy) that significantly contributed to suppression across all years of study. These can be understood in the context of size-asymmetric competition, as larger plants have a greater capacity to acquire resources than a smaller neighbour and the competitive advantage therefore becomes progressively greater through the season (Weiner & Thomas, 1986).

Christensen (1995) found that faster developing cultivars of spring barley were better suppressors of weeds. The importance of early height over mature height was demonstrated by Ogg and Seefeldt (1999), where the most tolerant and suppressive cultivars in the presence of *A. cylindrica* were those that increased height at a faster rate. These were the tallest cultivars during growth (but not necessarily at maturity). Other studies have found that wheat cultivars with late spike emergence were less tolerant of weeds (Huel & Hucl, 1996; Mason *et al.*, 2008). There would be value in further understanding the processes driving crop – weed interactions at this key developmental stage.

1.4.4 Stem production

Crop tillering as a trait in competition is commonly measured in three different ways:i) rate of tiller production, ii) final stem number, and iii) tiller economy (% of tillers surviving). Rate of tiller production and final stem number are morphologically plastic and density dependent; stem numbers reduce with increased inter and intraspecific competition. This has been demonstrated in wheat, barley and oats, and can vary between cultivars (Huel & Hucl, 1996; Seavers & Wright, 1997; Champion *et al.*, 1998). This translates to fertile head production and, consequently, yield reduction in weedy scenarios (Kirkland & Hunter, 1991; Satorre & Snaydon, 1992). Therefore, if tiller loss is not taken into consideration, tiller counts and rate of tillering from individual plants as a trait in crop-weed interactions may give misleading results.

The difficulty in separating density dependent effects from the innate capacity of cultivars to produce and maintain tillers may explain the lack of agreement between studies regarding the contribution of tiller number to competitive ability. Tillering capacity in wheat contributed to suppression of dry matter production in mixed weed assemblages (Korres & Froud-Williams, 2002). Challaiah *et al.* (1986) confirmed the negative relationship between tiller number and seed production of *B. tectorum,* but this was not consistent across sites. Higher tiller numbers also reduced seed production of *L. rigidum* in Australia (Lemerle *et al.*, 1996). Other work indicates that tiller number has little or no value in suppressing weeds (Moss, 1985; Wicks *et al.*, 1986; Champion *et al.*, 1998; Didon & Bostrom, 2003). It may be that the benefit of greater tiller number will be most evident at low crop densities, where they may increase the shading ability of the crop stand (Hoad *et al.*, 2006) – see

section, below, on integrating competitive cultivar traits with other cultural control options. Tiller economy in weedy situations would benefit from further study. This may be considered, in itself, a tolerance trait (as it indicates maintaining yield under competitive pressure), but also a suppressive trait due to a cultivar's ability to maintain high levels of light interception (Challaiah *et al.*, 1986). This was demonstrated by Seavers & Wright (1999), where cultivars with greater tiller economy were those with a superior suppressive ability.

1.4.5 Canopy architecture

Various facets of canopy architecture have been measured using a range of methods that can be difficult to reconcile. In wheat and barley, leaf area index at early growth phases was associated with suppression (Huel & Hucl, 1996; Hoad *et al.*, 2006; Hansen *et al.*, 2008). Coleman *et al.* (2001) quantified various potential measures of canopy architecture, and concluded that canopy height, width and length of leaf two, tiller number and size of flag leaf all contributed to suppressive ability, but relative importance differed between the two years of study. Seavers and Wright (1999) noted the importance of leaf size, combined with canopy height and tillering, in a study of wheat, barley and oats in competition with *G. aparine*, and compared the growth form of two wheat cultivars. The more erect cultivar with upright leaves was less suppressive than the cultivar with larger, less-rigid leaves, but only in one of the two years of study. However, Paynter and Hills (2009) could not explain differences in barley competitive ability against *L. rigidium* with growth habit or associated traits such as plant height and tiller number.

In some cases, a PAR meter has been used to quantify the level of light penetration, capturing the combined effect of these

variables. Such devices confirm that the most suppressive cultivars are those that intercept the most PAR (Didon & Hansson, 2002). Taller cultivars do not always transmit the least PAR through their canopies (Blackshaw, 1994), but often height does relate to PAR interception (Gooding *et al.*, 1993; Champion *et al.*, 1998). Measuring PAR may present a simple way to assess the suppressive ability of a cultivar. However, increased shading is also the primary mechanism by which increased seed rate suppresses weeds, as it influences canopy structure at a population level, thus any studies must take into account stand density and other factors such as row width.

Cereal leaves differ in their arrangement during growth (Davies *et al.*, 2004). The importance of structure at different growth stages is significant when its interaction with cultivar is considered (Hoad *et al.*, 2008). Cultivars that are planophile at the early growth stages have been shown to be more suppressive (Huel & Hucl, 1996; Hoad *et al.*, 2006). Challaiah *et al*. (1986) measured wheat canopy diameter in early June, and found that, when coupled with height, it provided a good means to predict competitive outcomes. Leaf angle in spring barley at growth stage 65 was indicative of suppressive ability (Hansen *et al.*, 2008). Changes in canopy architecture through the season also need to be interpreted in the context of the growth habit of different weed species. How canopy architecture contributes to tolerance abilities is less clear. High leaf area index indicates higher tolerance in some studies (Zerner *et al.*, 2008), but not others (Huel & Hucl, 1996).

1.4.6 Belowground traits

In comparison with aboveground canopy measurements, belowground traits have received relatively little attention in cereal crop-weed interactions. This is partly due to the

difficulties associated with measuring root traits. However, studies have indicated that root competition can be stronger than competition for light, particularly for nitrogen (Exley & Snaydon, 1992; Satorre & Snaydon, 1992; Lucas Bueno & Froud-Williams, 1994; Stone *et al.*, 1998). Studies on other species have suggested that traits such as root length density, root elongation rate, number of root tips and total root length are determinants of competitive outcomes (Fargione & Tilman, 2006; Stevanato *et al.*, 2011). At present, limited variation in root traits between cereal cultivars has been quantified (Satorre & Snaydon, 1992; Lucas Bueno & Froud-Williams, 1994). As techniques for measuring root growth develop, understanding of how root traits contribute to suppressive ability and tolerance in cereals is expected to improve.

Low input systems (such as organic agriculture) are more likely to suffer mineral deficiencies and there could be more potential in developing cultivars that are more competitive for belowground resources. In an experiment comparing the relative importance of aboveground and belowground traits of *Arabidopsis thaliana* (L.) under different nutrient regimes, belowground traits contributed significantly to suppressive ability in nutrient-poor conditions (Wang *et al.*, 2010). The ability to forage for water is vital in many locations, and may become increasingly important for determining the outcome of crop - weed competition in the context of predictions of widespread drought as a result of climate change (Stratonovitch *et al.*, 2012).

Due to difficulties in their measurement, belowground traits will not be studied in this thesis, apart from during the seedling growth stage. However, their potential contribution to competitive outcomes will be considered throughout.

1.5 **Competitive ability trade-offs**

It is not possible for a species to be maximally productive under all potential biotic and abiotic stresses. As such, species tend to evolve to attain high fitness in particular niches, often at the expense of traits that would provide a fitness advantage under a different scenario (Stearns, 1989). Such trade-offs have been exploited in commercial varieties of wheat. Semi-dwarf cultivars possess genes related to insensitivity to gibberellic acid, resulting in higher yield than taller cultivars in high-input, weed-free situations due to increased partitioning to grain (Sinclair, 1998), but are often poorer competitors under weed pressure (Challiah *et al.*, 1986; Siddique *et al.*, 1989). This has been associated with reduced height and early leaf area development (Rebetzke and Richards, 1999; Coleman *et al.*, 2001).

There is evidence that the trade-off between weed competition and yield potential is not inevitable. Huel & Hucl (1996) found that wheat cultivars with a high ability to withstand yield losses in weedy scenarios do not always rank low for weed-free yield, implying that a trade-off for tolerance need not necessarily be an impediment to breeding for competitive cultivars. Other studies suggest that breeding for suppressive ability and weed-free yield is a possibility in barley (Christensen, 1995; Bertholdsson, 2011), and in wheat (Coleman *et al.*, 2001; Vandeleur & Gill, 2004).

The case for the importance of considering trade-offs in cultivar breeding efforts is strong. However, trade-offs observed between traits are often more complicated than they initially appear (Roff & Fairbairn, 2007). Attention needs to be given to other traits that confer greater competitive ability, seeking any potential trade-off with other, fitness-related traits. For example, there may be trade-offs between cultivar competitive

ability and capability to resist stresses (Jordan, 1993). Such stresses could include limitation of resources other than light and space (such as water or minerals), resistance to crop pathogens, and climatic extremes (Grime, 1977). Work with *A. thaliana* suggests that lines with resistance to disease are less competitive in disease-free scenarios than their susceptible counterparts (Damgaard & Jensen, 2002).

One trait under investigation is early vigour. There is concern that increased early vigour would result in reduced winter hardiness, but these were not correlated in winter barley, implying no yield loss through increased frost susceptibility could be expected (Bertholdsson, 2011). But it has been suggested that, in drought conditions, early vigour would result in rapid assimilation of all available soil moisture, leaving the resource limited during grain filling (Lemerle *et al.*, 2001). It is pivotal that the understanding of trade-offs between traits related to competitive ability and weed-free yield is as complete as possible. Win-win traits that improve competitive ability without compromising other plant functions would be most desirable, as would an understanding of how their competitive strength may be specific to certain environments.

1.6 **Integrated management strategies**

Growing a more competitive cultivar alone will not solve the problems associated with the challenging conditions for weed control. Their use will need to be integrated with other cultural control strategies and the prudent use of herbicides. How cultivars interact with other weed control options needs to be considered. In this section, the focus is on delayed sowing and increased sowing rate in efforts to control *A. myosuroides*.

1.6.1 Time of sowing

Delayed sowing has been shown to decrease infestations of certain weed species in winter wheat (Christensen *et al.*, 1994; Cosser *et al.*, 1997). This is largely because a proportion of the autumn weed species germinate and may be controlled before the crop is sown, so fewer individuals germinate within the crop. The primary germination window for *A. myosuroides* is September and early October, with a small flush common in the spring. In its control in UK cereal crops, delaying drilling until as late as November can substantially reduce *A. myosuroides* emergence. The success of delayed drilling will vary depending on both weather conditions at the time of sowing, as well as the degree of primary dormancy the seed possesses that year (S. Moss, pers. comm.). The most extreme tactic is to sow a spring crop. In one study, switching from autumn-sown to spring-sown wheat resulted in a 78-96% reduction in plant populations (Moss & Hull, 2012). Reduced competitive ability is also reported in *A. myosuroides* emerging later in the autumn (Melander, 1995).

Farmers are often unwilling to delay autumn sowing. In unfavourable autumns, attempts to delay drilling may result in failing to drill the crop altogether. When late drilling is accomplished, the crop may yield lower as there is less time for wheat to tiller and due to poor establishment (though this can be partially offset by increasing the sowing rate). This is of particular concern in the UK, where heavy soils are commonplace on arable land (Lutman *et al.*, 2013). These yield penalties are unlikely be the same across cultivars, and any differences may be attributable to traits. Variation in rate of development between cultivars means they may differ in their ability to maintain competitive ability at different sowing dates,

and a high rate of growth may become more important when cereals are sown late (Hoad *et al.*, 2006). Faster developing cultivars may have a role to play in mitigating the risk to yield.

1.6.2 Sowing rate

A popular method of weed control amongst arable farmers is to increase sowing rate. This is due to the low cost of application compared to other control methods, and it does not carry the same risks as delayed sowing. It works on the principle that a greater mass of crop is present to compete against weeds, granting the population an asymmetric advantage to gather more resources and so further increase its advantage over weed populations (Weiner & Thomas, 1986). Increased seed rate has been observed to suppress weed growth in wheat (Christensen *et al.*, 1994; Grundy *et al.*, 1997; Champion *et al.*, 1998; Roberts *et al.*, 2001; Korres & Froud-Williams, 2002) and barley (Paynter & Hills, 2009; Auskalniene *et al.*, 2010). Mennan and Zandstra (2005) found that yield increased under higher sowing rates for wheat with and without competition from *G. aparine,* and at higher densities, greater suppression of the weed was achieved. In contrast, Moss (1985) reported higher yields and greater suppression of wheat at higher sowing densities in weedy conditions but did not report yield benefits in weed-free situations.

Many studies have found that sowing rate did not change the competitive rankings of cultivars in wheat (Cousens & Fletcher, 1990; Kirkland & Hunter, 1991) and barley (O'Donovan *et al.*, 2000). Doubling the sowing rate reduced *L. rigidum* biomass by approximately 25% across a wide range of wheat cultivars (Lemerle *et al.*, 1996), suggesting that it is a strategy highly compatible with the use of competitive cultivars. Other work has identified wheat cultivars that do not benefit from increased

density (Korres & Froud-Williams, 2002). This may indicate that, in some circumstances, low-density stands are able to intercept light as well as denser stands. Traits such as tillering ability may vary in effectiveness depending on weed density, which could explain differences between study results (Mason *et al.*, 2008).

The interactions between cultivar traits and other cultural control options are likely to be complex and interact with weather (see section 1.6). Predicting the relative benefit of contrasting combinations of cultivar, sowing date and seed rate in a variable environment can benefit from the application of models of crop - weed competition (Kropff & Spitters, 1992, Deen *et al.*, 2003, Storkey & Cussans, 2007). Two such models, one empirical and one mechanistic, used in this study are introduced below.

1.7 **Modelling crop - weed competition**

Various models have been proposed for predicting the outcome of competition in crop - weed scenarios. Often these are concerned with understanding the processes driving competitive dynamics and how management practices influence the outcomes, but are often too complex for application in the field or modification by other researchers. In contrast, simplified models with a practical application risks inaccuracy of the predictions. Acquiring a balance between research and practical models can be a challenge (Weaver, 1996).

In this project, two models were employed. One is the Relative Weed Green Area (RWGA) model, which is concerned with establishment and growth rates during the exponential growth phase. The second is the more comprehensive INTERCOM model, which builds upon the RWGA model by considering

factors influencing competitive outcomes once resources becoming limiting.

1.7.1 The Relative Weed Green Area model

1.7.1.1 *Relative growth rate in competition models*

The Relative Weed Green Area model focuses on the relative dominance of a crop - weed stand during the exponential growth phase, prior to resource limitation. As such, it utilising information on the seedling vigour of the species in question.

Seedling vigour can be split into three components – seed mass, emergence, and seedling relative growth rate. Seedling relative growth rate has been shown to be an important parameter determining the outcome of weed competition from modelling studies (Kropff & Spitters, 1992). Relative growth rate (RGR), is a measure of the rate of material acquisition per unit material per unit of time and a component of vigour. It is most commonly described in terms of total weight, where it is denoted in terms of grams per gram per unit time (for example, g^{-1} g^{-1} d^{-1}). It may also be applied to area (for example, plant green area).

The potential value of RGR in making predictions about the competitive ability of a species has been utilised in ecological theory, such as by Grime (1979) who outlined three key life history strategies typically employed by plants: competitors, stress tolerators and ruderals. This is part of a body of theory that has been discussed extensively in the literature, but the interest here is solely in RGR and its contribution to competitive ability in the context of the habitat of an arable field. In this system, fields are prepared for the mass germination of the crop. This closely simulates early successional environments in nature, where a high RGR is suggested to promote a high initial competitive advantage, a characteristic of the ruderal ecological

strategy (Grime & Hunt, 1975). Therefore, a model utilising components of seedling vigour, such as RGR, would operate by considering the growth of two competing species during the exponential growth phase – the time prior to the onset of competition between the species. The higher the proportion of space or area dominated by the crop, the lower its yield losses.

The importance of seedling vigour in competitive interactions has been implied previously in this literature review, making a compelling argument for its inclusion in models predicting crop yield loss.

1.7.1.2 *Components of RGR*

Relative growth rate is a product of a number of inter-related ecophysiological traits, displayed in Figure 1.2. These traits are the result of morphology (due to biomass partitioning) and physiology. The two main components of RGR are net assimilation rate (NAR) and leaf area ratio (LAR). The NAR is an indirect measure of the carbon gain per unit leaf area, taking into consideration its acquisition through photosynthesis and loss through respiration, exudation and volatilization, and as such considered a physiological component (Poorter, 1989). The LAR is a measure of green area, which is a result of SLA, the morphological component, and LWR (sometimes called 'leaf mass ratio'), the measure of resource allocation to the leaves (Poorter & Van der Werf, 1998). In some studies, the 'stepping stone' trait LAR is not examined, and only the direct contribution of SLA and LWR to RGR is considered (Shipley, 2002; 2006).

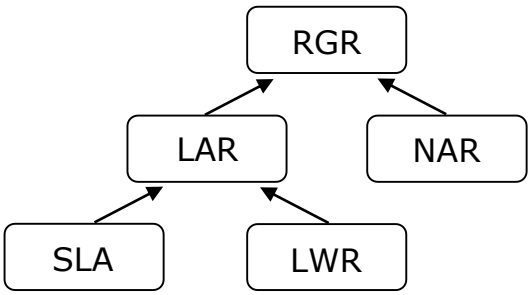

Figure 1.2 - the traits related to RGR.

Values for the ecophysiological traits vary in their ease to calculate. The more simple are SLA (leaf area / leaf dry weight), root weight ratio (RWR; root dry weight / total dry weight), LAR (leaf area / total dry weight) and LWR (leaf dry weight / total dry weight). Net assimilation rate (NAR) is calculated via the following equation:

$$NAR = \frac{W_2 - W_1}{tt_2 - tt_1} \times \frac{InL_2 - InL_1}{L_2 - L_1} \qquad (1.1)$$

Where L = leaf area; W = total plant dry weight; t = accumulated thermal time; $_1$ = first measure of given value and $_2$ = last measure of given value

NAR and RGR can be calculated as a function of chronological time but, here, thermal time is used to capture the effect of the environment on these rates. An arrangement of accumulated thermal time was calculated as follows:

$$tt = \Sigma\,(T_i - T_b) \qquad (1.2)$$

Where T_i is mean air temperature on day $_i$ and T_b is the base temperature of development.

The NAR, LAR, SLA and LWR have all been identified as drivers for RGR, though the frequency and strength of their determining RGR varies across studies. There are instances

where RGR is highly positively correlated to LAR, and was attributed primarily to SLA, whilst NAR made no discernible contribution (Poorter & Remkes, 1990). Other studies identified NAR as a key contributor to RGR (Shipley, 2002; Fu *et al.*, 2012) as well as the differing importance of each over seasons (Storkey, 2004). LWR has been linked to RGR, though to a lesser extent (Shipley, 2006).

It has been suggested that the components of RGR vary in their contribution as a result of environmental conditions. One such is irradiance, with a study reporting SLA being the most important component of RGR below 20 mols m^{-2}, whereas NAR is the strongest driver above 20 mols m^{-2} (Shipley, 2002). In an examination of 83 experiments, Shipley (2006) attributed different contributions of NAR and SLA to different light environments. Another is temperature, with SLA becoming the strongest contributor to RGR as temperatures increased from 18 to 28°C in a study of 16 species (Loveys *et al.*, 2002). In subarctic and alpine *Poa* species RGR was linked to LAR from 7 to 12°C and NAR from 12 to 17°C (Medek *et al.*, 2007).

The contribution of RGR to competitive outcomes is firmly positioned in ecological theory (Grime, 1977; Tilman, 1987). But, thorough examinations of RGR, differences between agricultural cultivars have been lacking. This is despite the fact that analyses of the drivers of crop / weed competition have identified seedling RGR as being a particularly important trait. If RGR provides a competitive advantage, in terms of both yield maintenance under competitive pressure and ability to suppress neighbouring weeds, then it could become a viable target for breeding. To do this, the key component of RGR in wheat cultivars should be identified and examined for any potential yield trade-off.

1.7.1.3 *The development of RGR-based models*

To acquire the maximal benefit out of an herbicide application, crop / weed competition models have been developed based on the principle of the economic threshold. Long-term economic thresholds are defined by Cousens (1986) as "the density above which weeds should be controlled in order to optimise returns over a number of years". As such, these models are focused on the ability of the crop to retain yield under a given density of weed. If models can predict economic thresholds for a given crop / weed competition scenario, the potential use of both could provide tools that allow growers to optimise their herbicide applications to their specific situation (Brain *et al*., 1999). In this thesis, data on the seedling RGR of different cultivars is used in the models to predict the potential impact of differences in cultivar seedling vigour on competitive ability.

1.7.1.4 *The density-based hyperbolic models*

Density of the crop and weed is a frequently adopted means of determining the outcome of competition. A widely-accepted description of the relationship between yield loss at given levels of weed density is the rectangular hyperbola (Cousens, 1985a; Ali *et al.*, 2013) (Figure 1.3).

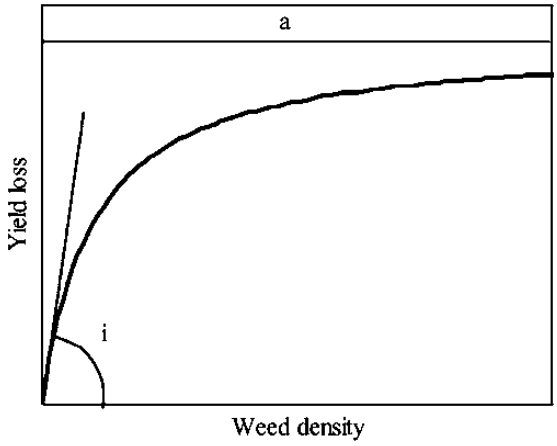

Figure 1.3 – The rectangular hyperbola, as described by Cousens (1985a), relating relative yield loss to weed density.

With this, the addition of each weed individual to a crop stand produces a reduction of yield, and its impact is additive until a weed density is reached where intraspecific competition starts to occur. Thereafter, the competitive impact of each subsequent individual decreases until an upper yield penalty plateau is reached. With a known weed density, yield loss predictions can be made (Equation 1.3).

$$YL = \frac{iWD}{1+iWD/a} \quad (1.3)$$

Where *WD* is weed density and *i* represents yield loss per weed per m^2 as density of the weed population approaches zero and *a* is percentage yield loss as $WD \rightarrow \infty$.

The model was further developed to include crop density as a parameter (Cousens, 1985b). This was accomplished by incorporating crop density into the *i* parameter. Using data from Hakansson (1983), where the yield loss caused by weeds to barley at various different crop densities was recorded, the parameter *i* could be estimated in each instance. A decrease in *i* behaved in a similar manner to yield loss observations at a constant crop density – increasing crop density can only increase yield so much, before intraspecific competition begins to limit further yield increases to a plateau.

Up to this point, the model assumed that the weed and crop would emerge simultaneously. This is not a frequent occurrence in reality, and relative time of emergence is an important aspect of seedling vigour as it determines the initial size of the crop and weed species, resulting in differences in yield loss (Knezevic *et al.*, 1997; Sarabi *et al.*, 2013). This impacts the value of

parameter *i*, with an increase the later the weed emerges after the crop. Cousens *et al.* (1987) added the effect of time of crop and weed emergence to the model by allowing the *i* parameter to change in accordance to relative time of emergence However, weeds frequently emerge in flushes, resulting in weeds of different sizes. Emergence flushes also mean that the necessary weed density counts, a time-consuming endeavour, can differ depending on when counts are taken. Suggestions on rectifying this issue included discarding density counts in favour of measures of early vigour. Biomass has been suggested as one such measure, as has leaf area and ground cover (Lutman *et al.*, 1996). The potential solution discussed and utilised here was to replace density counts with measures of green area (Kropff & Spitters, 1991).

1.7.1.5 *The two-parameter relative green area model*

Kropff and Spitters (1991) proposed a model based on the hyperbolic yield density function (Equation 1.4), replacing weed density counts with relative weed leaf area index (L_w). Using L_w is potentially a more powerful approach than density as it captures the three components of early vigour that are known to vary between crop cultivars weed species and weather conditions; initial seedling size, relative time of emergence and RGR.

The initial regression model is based on the principle that the relative leaf area of a species at the time of canopy closure is a strong determinant of the light capture and, thus, competitive strength of that species. This was equivalent to that found in equation 1.3, replacing plant density per m^2 with L_w, which is calculated as;

$$L_w = \frac{LAI_w}{(LAI_w + LAI_c)} \quad (1.4)$$

Where LAI_w is weed leaf area index and LAI_c is crop leaf area index.

The model was extended to include two parameters by Kropff *et al*. (1995):

$$YL = \frac{q\ L_w}{1+\left(\frac{q}{m-1}\right)L_w} \quad (1.5)$$

The refined model included the relative damage coefficient *(q*) (Kropff & Spitters, 1991) and a parameter quantifying maximum yield loss in the given scenario (*m*).

The *q* parameter is described as yield loss per unit leaf area at low weed densities, and when combined with data on crop and weed RGR (see below) allows the model to capture the effect of seedling vigour on competitive ability. It quantifies the effect of both weed density and the time between crop and weed emergence (Kropff & Spitters, 1991). However, unlike the parameter *i* in the density-based model, if the crop and the weed have different relative growth rates, L_w is dynamic and the parameter *q* will change depending on the time of assessment. During the exponential growth phase, this effect can be modelled if data are available on RGR:

$$q = q_0 \times \exp\left(\left(RGR_{crop} - RGR_{weed}\right) tt\right) \quad (1.6)$$

Where q_0 is *q* when L_w is at *tt* =0. The parameter *q* will be constant in time when the crop and weed have the same RGR.

The relationship between RGR and accumulated thermal time is used to account for germination flushes by eliminating the need

to rely on a carefully selected single time point assessment of crop and weed relative green area.

The additional parameter (*m*) aimed to rectify the maximal 100% yield loss prediction permitted under the single-parameter model, which is often unrealistic. Its influence is on the yield loss asymptote. The new parameter would prevent predictions of yield loss that were highly unlikely to occur in given crop – weed scenarios (such as 100% yield loss). It produced more accurate predictions in five of nine datasets tested when compared to the model lacking the additional parameter (Kropff *et al.*, 1995).

This model allows assessments to be made early in the crops growth, prior to canopy closure, as long as it has been parameterised for the crop and weed species in question. The model has been evaluated in numerous crop-weed combinations. *Chenopodium album* (L.) and *E. crus-galli* were successfully linked to yield loss in sugar beet (*Beta vulgaris* L.) and maize (*Zea mays* L.) respectively (Kropff & Spitters, 1991), and found to be an improvement on the weed density model (Kropff *et al.*, 1995). Relative leaf area models have been used to assess the ability of rice (*Oryza sativa* L.) (Bastiaans *et al.*, 1997) and canola (*Brassica napus* L.) cultivars (Langeroudi & Kamkar, 2009) to withstand the competitive impact of weeds, and found to give reasonable predictions of their performances in field trials. It has also been modified to assess yield loss in the presence of multiple weed species (Kropff & Spitters, 1991). However, these models are infrequently used to predict yield loss differences between cultivars under competitive pressure.

With predictions derived from the model, decisions can be made about weed management. It is also useful for quantifying the

potential impact of changing crop RGR on the outcome of competition. However, if management decisions extend into the period beyond the exponential growth phase, the simple relationship between *q* and RGR based on thermal time breaks down and a more complicated model such as INTERCOM is required.

1.7.2 The INTERCOM model

As previously discussed, the RWGA model uses a regression equation to predict the outcome of competition between crop and weed. But due to its focus on the exponential growth phase, it is deficient if one wishes to understand the underlying processes that determine competitive outcomes at different times of the year.

A model that aims to account for competition during and following the exponential growth phase is INTERCOM (Kropff & Spitters, 1992; Kropff *et al.*, 1992). INTERCOM is possibly the most studied simulation model of crop-weed competition, and has been parameterised for several crop and weed species since its inception (Weaver, 1996; Zimdahl, 2004). It considers environmental factors pertinent to competitive outcomes, such as light, temperature and water availability, and the allocation of resources between species of interest.

Mechanistic models of this type (based on underlying biological processes) have three kinds of variables. State variables are measurable quantities, such as green area or biomass. These measures are associated with rate variables, which quantify the change of state variables and their value at given moments in time. Rate variables are a measure of resource flow, and are often associated with photosynthesis and respiration. Driving variables are the external factors that influence rate variables

and, by proxy, state variables. Driving variables included temperature and water availability, and so represent the resources that plant species will be competing for. Driving variables influence rate variables, which go on to determine the state variables that influence competitive ability. Together these three variable classes are used by models like INTERCOM to make predictions of the outcomes of competition (Kropff & van Laar, 1993).

As further driving variables are included, a model must become increasingly sophisticated. The breadth of inputs required for these models often limits their application at the farm level. Model development often seeks to find a balance between simplicity and the necessary complexity to improve simulation of real-world scenarios. The model by Kropff and Spitters (1992) was devised with this in mind. It aimed to understand the mechanisms underlying competition with practical solutions as a core principle. These include identifying crop traits that may be of interest to breeders and how management techniques influence the crop-weed system.

The primary driving variables included in the model are light, temperature and available water, all of which are growth-limiting. A representation of the model is presented in figure 1.2. The distribution of resources between species and the efficiency of resource uptake are central to plant species competition. Following the exponential growth phase (modelled as described in section 1.7.1), the ability of crop and weed to intercept light is determined through the share of the canopy (species LAI), leaf traits related to light absorption (such as angle), and the vertical distribution of leaf area through the canopy. The model also accounts for how these variables change over time. This information allows a daily CO_2

assimilation rate for each species to be determined, and once glucose production and respiration requirement accounted for, converted to net daily growth rate (kg dry matter ha^{-1} day^{-1}).

The limiting impact of water is determined through soil moisture and its allocation to the competing species in proportion to their needs. Precipitation and the soil water balance are included in the model, and rates of transpiration and evaporation are considered. Transpiration and growth will decrease when soil moisture falls below a pre-determined level.

The model splits the period of cultivar growth into sections based on phenological development – the exponential growth phase, overwintering/rapid spring growth, and senescence. These phases represent changes in how the crop partitions available resources, thus simulations need to change in accordance with developmental phase. Transition is dependent on ambient temperature, sometimes in combination photoperiod, depending on the stage and plant species. Prior to canopy closure (and, therefore, the onset of competition), this is a result of daily temperature. Plant height growth is predicted to follow the logistic function against sum temperature, as defined by Spitters (1989).

The model was initially developed for spring-sown sugar beet – *C. album* (Kropff & Spitters 1992). The simulation model was tested using sugar beet and *C. album* across experiments run over three growing seasons with notably different weather conditions, with sugar beet yield losses ranging from -6% to 96%. The simulation model explained 98% of the variation in yield loss (Kropff *et al.,* 1992).

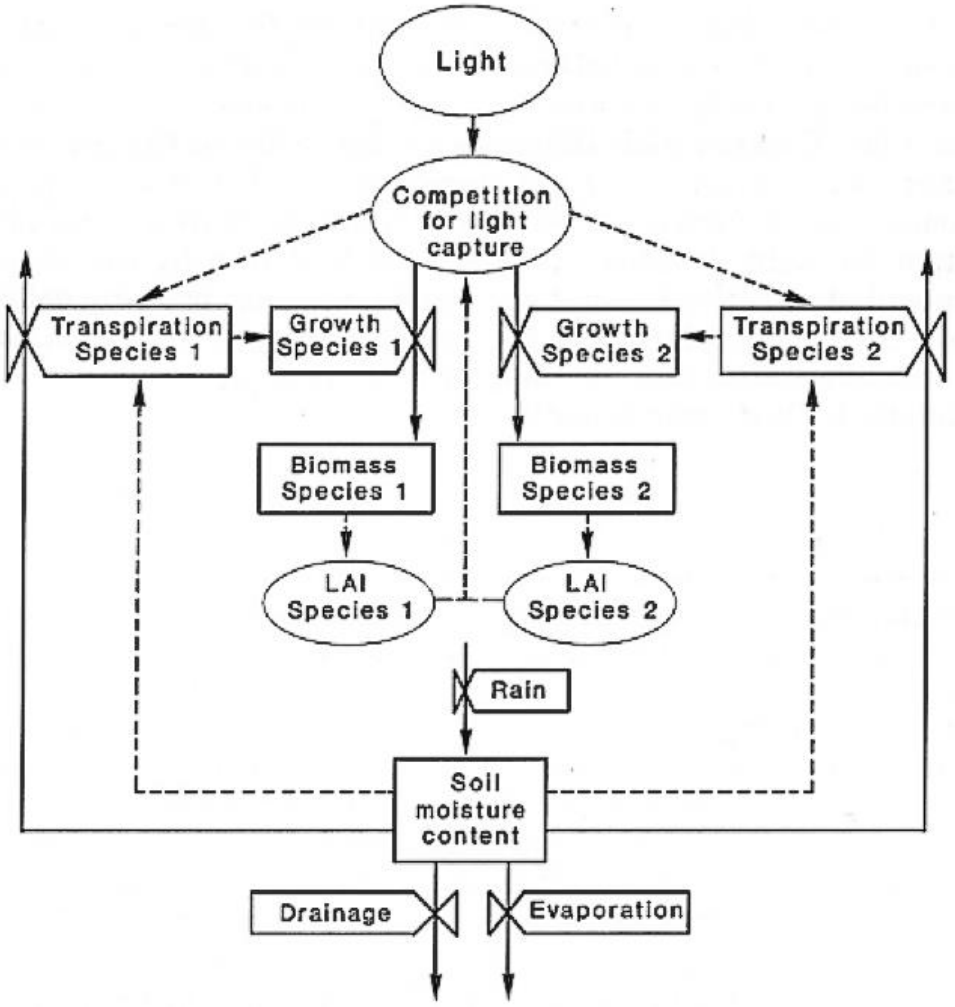

Figure 1.4. – A diagrammatic representation of the functioning of the INTERCOM model, taken from Kropff & van Laar (1993).

1.7.2.1 *Sensitivity analyses*

It is very difficult to untangle the influence of different plant traits on competition for limiting resources. The INTERCOM model is a powerful tool for identifying the importance of different traits (and their interactions) in determining the outcome of weed competition and the effect of the environment and will be used later in this thesis. Establishing what traits grant an increased competitive ability could provide useful insights for weed management strategies and provide targets for selective breeding.

Kropff *et al.,* (1992) ran a sensitivity analysis on traits in sugar beet, to assess which had the strongest influence on predictions of percentage yield loss when in competition with *C. album*. To do this, values were adjusted by 5%, and the subsequent change in yield loss noted in six competition scenarios. Changes to relative growth rate of leaf area, specific leaf area and height resulted in the largest changes in yield loss. This implies they are important components of competitive strength, with temperature between emergence and canopy closure being an important external determinant of competitive outcomes. This justified the use of these values in predictions of yield loss due to competitive interactions. Relative growth rate of leaf area was influenced by temperature in all six scenarios

1.7.2.2 *INTERCOM in wheat – A. myosuroides competition*

The INTERCOM model is a detailed model, justifying its own book (Kropff & van Larr, 1993), and so this section will focus on the updates and relevant parameters.

The version of INTERCOM used herein was parameterised for winter-sown wheat and *A. myosuroides* (Storkey, 2004; Storkey & Cussans, 2007). To account for a winter-sown crop, components of the crop growth model *Sirius* were integrated into the INTERCOM model (Jamieson *et al.*, 1998; Storkey & Cussans, 2007). Processes that had depended on sum temperature values, such as switches from one developmental stage to another, are instead mediated by photothermal time.

The exponential growth phase is modelled as described in section 1.7.1., a period with RGR_{GA} being a primary determinant of the share of the stand between wheat and *A. myosuroides* once a green area index (GAI) of 0.75 is reached. As such, this model represents the most simple of crop and weed growth

models, as all resources are assumed to be unlimiting, and plant growth is determined by temperature and relevant species characteristics such as RGR_{GA} and initial green area (L_0). Following this period, resource competition is assumed to begin.

The model calculates radiation absorption of crop and weed, using extinction coefficient. Extinction coefficient was calculated as demonstrated in the equation below.

$$I_{a,h,i} = k_i(1-p)I_0 exp\left(-\sum k_j L_{h,j}\right) \quad (1.7)$$

Where $I_{a,h,i}$ is the light absorption of species *i* (J m^{-2} s^{-1}) at height *h* (m), k_i the extinction coefficient for species *i*, *p* the reflection coefficient of the canopy, I_0 the radiation at the highest canopy point (J m^{-2} s^{-1}), k_j the extinction coefficient of species *j* and $L_{h,j}$ is the leaf area index of species *j* at height *h*. The equation describes the reduction of radiation reaching foliage as leaf area increases, following an exponential trend (Kropff & van Lar, 1993).

The model determines what resources are allocated to leaf area production, where in the canopy this is distributed and used the distribution of leaf area through the height of the canopy to calculate CO_2 assimilation of the species. Extinction coefficients as a measure of radiation capture also required an understanding of the vertical distribution of green area at five points of the canopy. Data on the distribution in wheat and *A. myosuroides* were acquired by Storkey, (2006). Proportion of total leaf weight through the canopy fit a parabolic function in wheat and a rectangular function in *A. myosuroides*.

Assimilation rate, which has been described on a per hour (gross assimilation rate) and per second (instantaneous

assimilation rate), is a measure of the ability of the whole-plant to intercept light and uptake carbon. INTERCOM calculated the gross assimilation rate (kg CO_2 ha^{-1} h^{-1}) using extinction coefficients at different levels of the canopy using initial light assimilation rate (ε) and maximum assimilation rate (A_{max}).

$$A_L = A_{max}[1 - exp(-\varepsilon H_h / A_{max})] \quad (1.8)$$

Where A_L is the gross assimilation rate (kg CO_2 ha^{-1} h^{-1}) and H_h is light absorbed at height h of the canopy. Calculating A_{max} for each species required separate parameters to describe how it responded to temperature. However, Storkey (2005) showed that the response of A_{max} to light and temperature can be predicted using SLA and leaf nitrogen content. This response allowed A_{max} to be calculated via the following equation:

$$A_{max} = \frac{(16.92 - 16.92 \times 0.88^T)N}{SLA} \quad (1.9)$$

Where SLA is specific leaf area (ha kg^{-1}), *N* is the proportion of leaf nitrogen to total leaf dry weight and *T* is leaf temperature.

1.8 Difficulties implementing competitive cultivars

1.8.1 Breeding for competitive ability

The potential to breed for competitive ability has been discussed in the scientific literature, but has seen little implementation in the industry. Within northwest Europe, demand for cultivars with increased yield dominates the market. The Agricultural and Horticultural Development Board recommended list (RL) for cereals in the UK puts particular pressure on breeders within the country, as RL candidateship is a strong driver of a cultivar's profitability. This pressure results in less attention being given

to other beneficial traits, especially competitive ability. A potential trade-off between competitive ability and other desirable traits may create reluctance to select for competitive ability, But the research discussed above imply that such trade-offs are not inevitable. Competitive cereal cultivars are noted as being unable to control problem weed populations predictably, owing in part to variation in their success across years (Cosser *et al.*, 1997). Such observations may weaken the perception of them being a viable control method and a profitable enterprise.

To make breeding a viable option, understanding of the traits dictating competitive ability and their relative contributions would benefit from further exploration (Pester, 1999). Furthermore, since natural selection acts on phenotypes, not genotypes, the conserved heritability of competitive traits needs to be demonstrated (Lande & Arnold, 1983). Work towards this goal has shown potential. Coleman *et al.*, (2001) identified traits in wheat that conferred suppressive and tolerance capabilities and used quantitative trait loci (QTL) mapping to identify hereditability. Phenotypic variation of important traits was only partially explained by genetics, but their locations on the chromosome were constant over the two years and often closely linked to one another. Later work showed that width of the first leaf has a high heritability and is linked to specific leaf area and early vigour, making it a potential target for breeding efforts (Rebetzke & Richards, 1999; Rebetzke *et al.*, 2004).

1.8.2 Screening for competitive ability

The idea of developing a ranking system for competitiveness of cultivars has been around for the past two decades. A screening protocol that predicts the competitive ability of cultivars would

ideally be based on simple and rapid assessment of a selection of suitable traits (Cousens & Fletcher, 1990; Olesen *et al.*, 2004). Such grading of cultivars should provide farmers with criteria to use when making management decisions (Lemerle *et al.*, 2001). It would be more practical than current procedures, where cultivars would require many years of testing over a variety of conditions to get an accurate measure of suppressive ability (Brain *et al.*, 1999). Farmers wishing to select a competitive cultivar often find that information on competitive ability is limited or anecdotal.

Hansen *et al*. (2008) were successful in producing predictive ranking criteria for suppressive ability in spring barley. It was developed based on four traits – red-far red light reflectance at growth stage 31, leaf area index at growth stage 65, angle of leaves and the length of the culm, and was validated independently. However, some changes in ranking were observed in this study during independent assessments in differing locations, weakening the predictions of suppression. Including additional early growth traits has the potential to improve screening protocols as they may have an important role in determining the competitive ability of cultivars but have received relatively little attention.

1.8.3 The impact of variable environments

Ranking for suppressive ability can change in studies conducted over multiple years (Vandeleur & Gill, 2004). But not all studies see variation. Didon and Hansson (2002) found across two years with differing rainfall and light availability, suppressive abilities were consistent for barley cultivars, but tolerance was not. These differences may be attributed to trait variation. Competitive traits vary in their impact between years (Christensen, 1995; Huel & Hucl, 1996; Cosser *et al.*, 1997;

Cousens & Mokhtari, 1998; Coleman *et al.*, 2001; Bertholdsson, 2005), due to crop or weed species response to weather conditions.

Various facets of an environment can influence competitive ability. A study of wetland species demonstrated that soil fertility and level of waterlogging influences their ability to tolerate competing species, but did not influence rankings of suppressive ability. However, suppressive ability changed with the species being suppressed, whilst tolerance did not (Keddy *et al.*, 1994). Traits did not always contribute to competitive strength of winter wheat cultivars – a result suggested as being due to their interaction with the environment, with differences in rainfall levels having a stronger impact on weed fitness. (Ogg & Seefeldt, 1999). Seasonal differences have been noted to influence tiller production and loss (Hoad *et al.*, 2006).

Weed species that may be identified as problematic will vary over large regions. Whilst *A. myosuroides* is the major challenge facing arable growers in the UK (Moss *et al.*, 2011), Australian growers contend with herbicide-resistant *L. rigidum* (Owen *et al.*, 2007). Cereal cultivars noted as competitive may lack broad effectiveness against all weed species (Grundy *et al.*, 1997). For example, Gooding *et al.* (1993) reported increased *Veronica hederifolia* (L.) in the presence of the study's taller cultivar. Other studies have suggested that competitive traits are not highly target-species-specific (Huel & Hucl, 1996; Didon & Hansson, 2002). There would be value in knowing if traits identified as suppressive will impact weed species of differing growth forms. This would require the examination of multiple weed species in competition with a selection of cultivars. At present, the majority of studies focus on a single weed species or weed assemblages without separating species.

Agroecological systems, whilst typically less complicated than natural ecosystems, are subjected to a variety of challenges that may differ over years and localities. In order to ascertain cultivar suppressive ability, the use of multiple traits could strengthen predictions, as different traits may have greater importance under particular conditions (Christensen, 1995; Mennan & Zandstra, 2005).

1.9 **Project Outline**

This thesis seeks to understand what wheat traits contribute to crop suppressive ability against weed species *A. myosuroides*. There are three key objectives to the project.

1. The relative contribution of above-ground traits in wheat to competitive outcome will be assessed. Suppressive ability of problematic weeds will be the focus. Traits that do not impose a yield penalty in weed free situations are of primary interest.
2. Information on the contribution of different plant traits will be used to produce a screening protocol. This will provide a means to quickly and non-destructively assess new cereal cultivars for competitive ability, providing a ranking much like that used by the Agriculture and Horticulture Development Board (AHDB) recommended list in regards to disease resistance.
3. The contribution of competitive cultivars in conjunction with weed control strategies such as delayed drilling and increased sowing rate will be assessed using simulation modelling in the context of variable environmental conditions.

1.9.1 Thesis contents

This thesis is divided into seven chapters. Chapter Two parameterised the Relative Weed Green Area model for cultivars in making predictions of cultivar competitive ability. Chapter Three details suppression studies of wheat cultivars based on outdoor sand-beds, identifying traits related to suppressive ability. Chapter Four repeats this experiment *in situ*, and considers tolerance. Chapter Five examines cultivar choice, delayed drilling and sowing rate, as well as suppression of weed species *Stellaria media* (L.). In Chapter Six, the INTERCOM model is parameterised for two cultivars to make predictions of competitive outcomes in variable environments. In Chapter Seven, results from the experimental chapters are summarised and conclusions drawn regarding the use of competitive wheat cultivars in *A. myosuroides*-infestation.

2 Chapter 2 - Quantifying the variation in seedling vigour between cultivars and the implications for crop / weed competition

2.1 Introduction

Evidence suggests that early seedling vigour can be a good determinant of species competitive ability, and traits related to vigour may be used to predict competitive ability. Seedling vigour can be split into three components – seed mass, emergence, and seedling relative growth rate (RGR). Seedling RGR has been shown to be an important parameter determining the outcome of weed competition from modelling studies (Kropff & Spitters, 1992).

2.1.1 The Relative Weed Green Area model

The Relative Weed Green Area model (RWGA) was developed to predict yield losses as a result of weed competition, to assist in weed management decisions. It was derived from the density-based hyperbolic yield loss model (Cousens, 1985a), using proportional dominance of the canopy by crop and weed at the end of the exponential growth phase (when green area index is 0.75) to predict crop yield loss. It does this by integrating RGR of the crop and weed into the *q* parameter, which has been found to adequately account for differences in cover that may result from weed flushes (further detail in section 1.7.1). This simple model has been calibrated for different crop - weed scenarios, but has rarely been applied to the cultivar level.

2.1.2 Components of RGR

To understand the role of vigour and exploit it in the breeding of superior competitors, it would be valuable to consider the ecophysiological traits driving RGR.

Relative growth rate is a product of a number of inter-related ecophysiological traits. The two main components of RGR are net assimilation rate (NAR) and leaf area ratio (LAR). The NAR is an indirect measure of the carbon gain per unit leaf area. The LAR is a measure of green area, which is a result of specific leaf area (SLA) and leaf weight ratio (LWR) (further definitions in Table 2.1).

Table 2.1 – Terms and descriptions of growth form analysis components

Abbreviation	Definition	Description	Units
SLA	Specific leaf area	A measure of leaf thinness	$m^2\ g^{-1}$
NAR	Net assimilation rate	An indirect measure of net carbon gain	$gm^{-2}\ d^{-1}$
LWR	Leaf weight ratio	Ratio of total weight allocated to leaves	n/a
LAR	Leaf area ratio	Ratio of leaf area to total plant biomass	n/a
RWR	Root weight ratio	Ratio of root weight to shoot weight	n/a
RGR_{GA}	Green area relative growth rate	The rate of green area growth per unit area per day	$cm^2\ cm^{-2}\ tt^{-1}$
RGR_W	Total dry weight relative growth rate	The rate of biomass growth per unit mass per day	$g\ g^{-1}\ tt^{-1}$

The NAR, LAR, SLA and LWR have all been identified as drivers for RGR, though the frequency and strength varies across studies (Poorter & Remkes, 1990; Shipley, 2002; Shipley, 2006; Fu *et al.*, 2012) and differ in importance with seasons and environmental conditions (Storkey, 2004; Loveys *et al.*, 2002).

The RWGA model has been parameterised for various crop - weed combinations, but there has been little work on the importance of cultivars. This chapter investigates how the predictions of % yield loss made by the RWGA differs between cultivars of wheat, barley and oat. The RWGA model is applied to commercial UK cereal cultivars, with a focus on wheat. The RGR for each cultivar will be quantified and used to parameterise the RWGA model.

If RGR provides a competitive advantage, in terms of both yield maintenance under competitive pressure and ability to suppress neighbouring weeds, then it could become a viable target for breeding. The key components of RGR will be identified for this purpose.

2.2 **Aims**

In this chapter, the following hypotheses will be tested:

1. There will be variation in relative growth rate (RGR) between the cultivars included in this study.
2. The differences in RGR can be associated statistically with other ecophysiological components, such as net assimilation rate (NAR), leaf area ratio (LAR), and LARs components, specific leaf area (SLA) and leaf weight ratio (LWR).
3. The Relative Leaf Area Model can be used to demonstrate the impact of RGR_{GA} on the competitive outcomes between wheat and *A. myosuroides*.

2.3 Materials and Methods

2.3.1 Experimental component

2.3.1.1 *Cultivar choice and seed sourcing*

Cultivars were selected after consultation with project partners, so that competitive ability and traits considered important were represented over a large spectrum. Some cultivars were selected based on anecdotal information and industrial trials implying either high or low competitive ability. Others were selected to gain a wide representation of traits suspected to confer competitive ability, such as differences in their rate of tillering, final tiller number and speed of development in the spring. Some information, such as final height, was available from the AHDB recommended lists. At the request of project funders, research focused on modern UK wheat cultivar.

The original project proposal was to examine cultivars of wheat, barley and oats, to gain an insight into the competitive ability of each species. Unfortunately, acquiring a suitable number of cultivars of barley and oats was not possible before the onset of the 2011-12 experiment, and only three barley and one oat were examined. In subsequent years, it was decided to restrict the focus to wheat so that a broad array of traits could be collected from a large pool of cultivars over the three study years. A single cultivar of barley and oat was included in 2012-13 and 2013-14 experiments for curiosity.

A total of 19 winter cultivars were included in the experiments conducted during the 2011/12 growing season. Sixteen were wheat (*Triticum aestivum* L.) cultivars Claire, Conqueror, Denman, Duxford, Gallant, Grafton, Hereward, Invicta, Ketchum, Kingdom, KWS Santiago, Maris Widgeon, Oakley, Robigus, SY Epson, and SY109056 (Torphins). The three barley

(*Hordeum vulgare* L.) cultivars were Sequel, Suzuka, and Volume. Gerald was the single oat (*Avena sativa* L.) cultivar used. All seeds were sourced from Syngenta UK in 2011/12, except Maris Widgeon, which was provided by Dr Debbie Sparkes (University of Nottingham).

In the 2012-13 growing season, the number of cultivars was reduced to 12 based on experience from the first growing season. Ten were wheat cultivars Claire, Conqueror, Duxford, Gallant, Grafton, Hereward, KWS Santiago, Oakley, Panorama and Robigus. Volume was the single barley cultivar and Gerald was the single oat cultivar. In 2012-13 and 2013-14, Conqueror, Grafton, KWS Santiago and Oakley were sourced from KWS UK Ltd; Duxford, Gallant and Volume were sourced from Syngenta UK; Panorama and Claire were sourced from Limagrain UK; Gerald was sourced from Senova.

Panorama and Hereward were not initially choices for ongoing experiments, due to their non-inclusion in the 2011-12 experiment, but unforeseen difficulties in sourcing seeds for two original choices (Ketchum and Torphins) required their prompt replacement with cultivars available at the Rothamsted Experimental Farm.

In order to parameterise the model effectively, cultivars that were present across all three years of experimentation were those included in the subsequent work. These were the wheat cultivars Claire, Conqueror, Duxford, Gallant, Grafton, KWS Santiago, Oakley and Robigus. The barley cultivar Volume and the oat cultivar Gerald were also included.

The relative green area model has been parameterised for *A. myosuroides* in the past using the wheat cultivar Mercia (Storkey *et al.*, 2003).

2.3.1.2 *Experiment description*

A total of 320 pots (90 x 90 x 95 mm) were filled with a 24% clay weed loam mixture (80% sterilized screened loam, 20% lime-free grit and 2kg m^{-3} of slow-release Osmocote ® mini slow-release fertiliser) and arranged in four columns that were 5 pots wide on sand-beds at Rothamsted Research. Each row was a different cultivar and the order was randomly determined. Each pot was sown by hand with three seeds to a 10 mm depth, and individuals were thinned down to one as they emerged. The pots were buried in sand to reduce levels of soil freezing to those more equivalent to what would be seen *in situ*. Sowing and harvesting dates for each year are listed in Table 2.2.

Sampling was done by randomly selecting one plant from each replicate column and removing it from the pot, gently loosening the soil around the roots and cleaning them with running water in a fine mesh sieve. Leaves and tillers were counted, and plants were dissected into uncurled leaves, green stem (curled, immature leaves included), pale stem and roots (Figure 2.1). Using the WinDIAS programme, a leaf area and green stem area measurement was acquired for each individual, and then leaves, stems and roots were dried at 80°C for a minimum of 18 hours. The dried material was weighed to four decimal places.

Table 2.2 - The sowing and harvest dates for the ecophysiological traits experiments. The greater time lapses between each sample date in 2012 were to account for lower autumn temperatures that limited seedling growth.

		Harvest number				
Year	Sow date	1	2	3	4	5

2011	10-11 Oct	25-26 Oct	2 Nov	8-9 Nov	15-16 Nov	23-24 Nov
2012	15-16 Oct	1 Nov	9 Nov	16 Nov	29 Nov	14 Dec
2013	17 Oct	30 Oct	6 Nov	12 Nov	22 Nov	2 Dec

Figure 2.1 - Two contrasting wheat cultivars, prepared for assessment of green area and resource allocation with four replicates of each.

2.3.1.3 *Ecophysiological traits*

Ecophysiological traits for each cultivar were determined from the raw data collected, and calculated. This data underwent Pearson's correlation analysis using Genstat 16th Edition, to seek significant relationships between the traits. Relative growth rates of dry biomass and green area, and W_0 (seedling weight at zero tt) and L_0 (seedling green area at zero tt) were included in the analysis.

2.3.2 The Relative Green Area Model

2.3.2.1 *Acquiring the parameters*

Using green area from multiple dates, RGR values for each cultivar were derived. Prior to the onset of competition and resource limitation, green area and dry weight accumulation over time follow an exponential trend. As such, RGR can be calculated from a linear regression of the natural logarithm of dry weight (for RGR_W) or green area (for RGR_{GA}) against time. Green area (including leaf and stem green area, as used by Storkey (2004)) were fitted to a linear regression against thermal time for the three years that the data was collected, to acquire values for RGR_{GA} and L_0 for each cultivar:

$$Ln(L) = Ln(L_0) + RGR \times tt \qquad (2.1)$$

$Ln(L_0)$ represents the intercept of the trend line with the x-axis, representing the trait at zero thermal time. This value is termed L_0 for initial green area and W_0 for total initial dry weight, and requires back-transformation for the value in its original units. Data acquired across all three experimental years were included to produce a single value (Table 2.3).

Accumulated thermal time was adjusted to a base of -0.4°C for *A. myosuroides*. This was in keeping with previous work carried out by Storkey *et al.* (2000), where the optimal base temperature of development for the species was derived for linear regressions of natural logarithm green area against accumulated thermal time. No adjustment was made to the cultivar base temperature due to the high goodness-of-fit at a base temperature of 0°C.

To predict green area of an individual plant cultivar at any given thermal time, RGR is utilised in equation 2.2:

$$Ln(L_0) + tt \times RGR_{GA} \quad (2.2)$$

Table 2.3 - Parameters used in the ecophysiological simulation model of the growth of cultivars and *A. myosuroides*. The RGR_{GA} used for *A. myosuroides* was 0.0108 (Storkey 2003)

	(Ln)L_0 (cm^2)	RGR_{GA} (cm^2 cm^{-2} tt^{-1})	R-squared
Claire	-0.45	0.0106	0.92
Conqueror	-0.34	0.0098	0.94
Duxford	-0.39	0.0116	0.91
Gallant	-0.27	0.0104	0.90
Gerald	-0.38	0.0094	0.85
Grafton	-0.51	0.0111	0.88
KWS Santiago	-0.34	0.0096	0.92
Oakley	-0.53	0.0107	0.87
Robigus	-0.27	0.0094	0.90
Volume	0.63	0.0088	0.82

The result can be used to predict stand green area by accounting for the density of plants per m^2 in equation 2.3:

$$(Ln(L_0) + tt \times RGR_{GA}) \times D \quad (2.3)$$

Where *D* represents the density of the stand (m^{-2}).

In Figure 2.2, the growth of two virtual plants is presented based on predictions utilising equation 2.3.

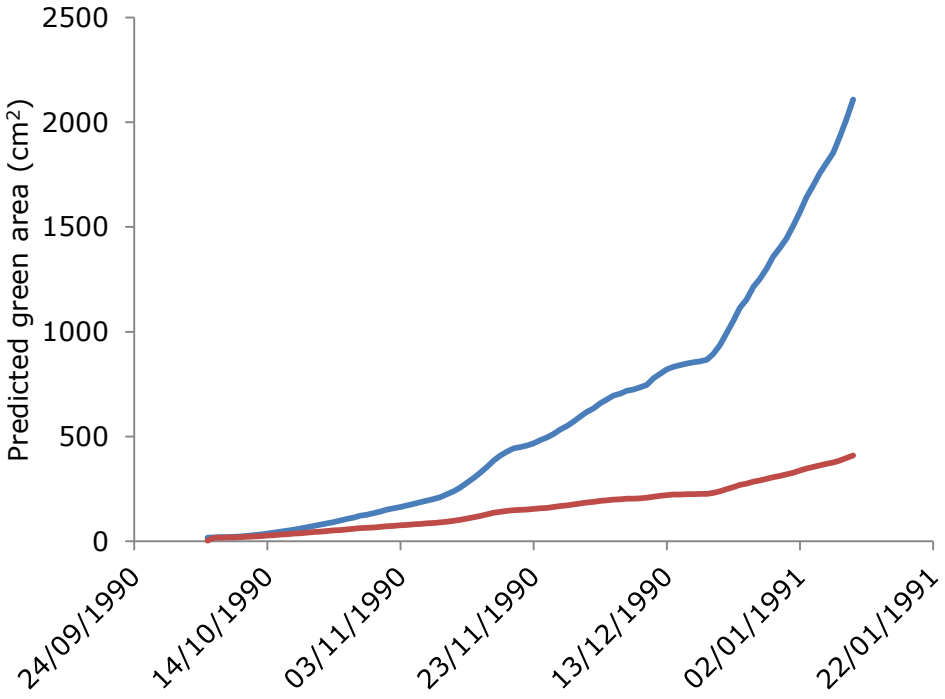

Figure 2.2 - The green area growth of two virtual plants during the exponential phase, as predicted by equation 2.3. Low RGR = Red (0.007 cm^2 cm^{-2} d^{-1}); High RGR = Blue (0.005 cm^2 cm^{-2} tt^{-1}). The difference in the RGR between two competing species will determine the value for G_w input into the RGA model. For the analysis of the impact of variation in RGR between cultivars, this was determined on the 10th January. The RGR of *A.myosuroides* was determined from previous work.

2.3.2.2 *Comparing variation in predicted yield loss due to cultivar differences and seasonality*

Having acquired values for RGR_{GA} and L_0, green area can be calculated for a standard crop and weed density on a given data using daily temperature data since emergence. Predictions of the expected % yield losses can be made for the cultivars in different temperature conditions (as demonstrated in Figure 2.2). To do this, historical air temperature data from the Rothamsted weather station was used, and thermal time calculated for the wheat and *A. myosuroides* (amended for base temperatures). A density of 186 m^{-2} was chosen for cultivars and 20 m^{-2} for *A. myosuroides*, in keeping with those used for the parameterisation of the model for wheat – *A. myosuroides* competition (Storkey *et al.*, 2003).

The model was run for the years 1990-1999. Predictions of green area were based on daily air temperatures between 4 October and 10 January. The resulting relative weed green area could then be used to make predictions of cultivar yield loss due to competitive pressure through the use of equation 2.4.

$$YL = \left(\frac{q\ G_W}{1 + \left(\frac{q}{m-1}\right) \times \left(\frac{GAI_W}{G_W}\right)} \right) \times 100 \qquad (2.4)$$

Where q is the relative damage coefficient, GAI_w is the weed green area index, G_w is the relative weed green area and m is the maximum yield loss expected at very high weed densities.

The value for q was 4.2 and m was 0.8, as determined from previous work on wheat and *A. myosuroides* (Storkey *et al.*, 2003). With a q value in excess of 1, it is indicated that *A. myosuroides* is a superior competitor to wheat (Kropff & Spitters, 1991). Work by Storkey and Cussans (2007) demonstrated that these parameters may be used to predict the yield loss of wheat when in competition with a weed across sites and years using data for a single cultivar.

The time at which predicted green area values are derived has important implications for the model. Often the crop and weed have dissimilar RGRs, resulting in the relative weed green area changing over time. Green area values increase at an exponential rate, resulting in a widening gap in green area observed between two populations with differing RGR_{GA} values (Figure 2.2). This result to changes to the predicted GAI_w – a central component to equation 2.4. In biological systems, this exponential growth would cease with the onset of resource competition and other traits start to become important, such as height. January 10 was chosen as an approximation of when

factors besides temperature begin to limit growth and resource competition, based on the previous parameterization of the RWGA model for wheat - *A. myosuroides* scenarios (Storkey *et al.*, 2003). For the purposes of this analysis, it is assumed that seedling vigour is the only trait that varies between cultivars to isolate the potential importance of this trait in determining competitive ability.

2.4 **Results**

2.4.1 Modelling RGR

Due to the irrigation provided to seedlings, watering was adequate for requirements in all three autumns. Temperature varied over the years, with mean temperatures during the experimental periods being 10.1°C in 2011, 6.4°C in 2012, and 8.2°C in 2013.

The use of linear regression to derive RGR_{GA} and RGR_{W} against thermal time was found to be appropriate on natural log-transformed values of green area and total dry weight (Figure 2.3 and 2.4). For RGR_{GA}, the coefficient of determination (R^2) was approximately 0.9 for the wheat cultivars. The oat (Gerald) and barley (Volume) cultivars had less good fit, at 0.85 and 0.83 respectively (Table 2.3). It is likely that the variance in these species would be better accounted for with a more appropriate base temperature, or use of effective day-degrees (which incorporates daily radiation values) as demonstrated by Storkey (2004).

Green area accumulated at a faster rate than total dry weight (Figure 2.3 and 2.4). The fit of dry weight was weaker (Figure 2.3). If it were to be included in modelling efforts, a more appropriate base temperature may have been applied to improve the coefficient of determination. Mean RGR_{GA} differed

between cultivars (Figure 2.5), with Volume (barley) and Gerald (oat) occupying two of the lowest-ranked positions.

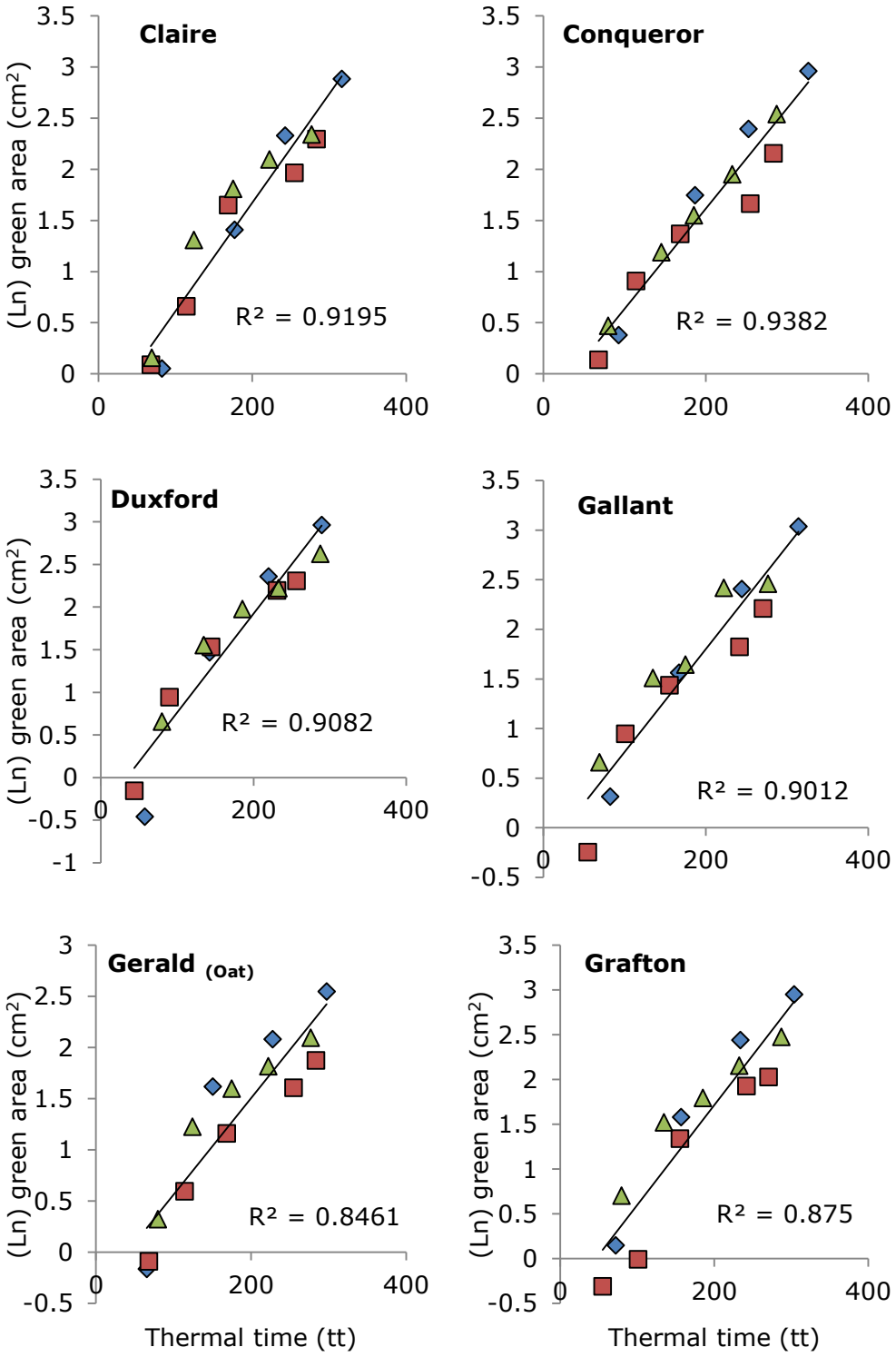

Figure 2.3a - Cultivar green area during autumn. ◆ = 2011, ■ = 2012, ▲ = 2013.

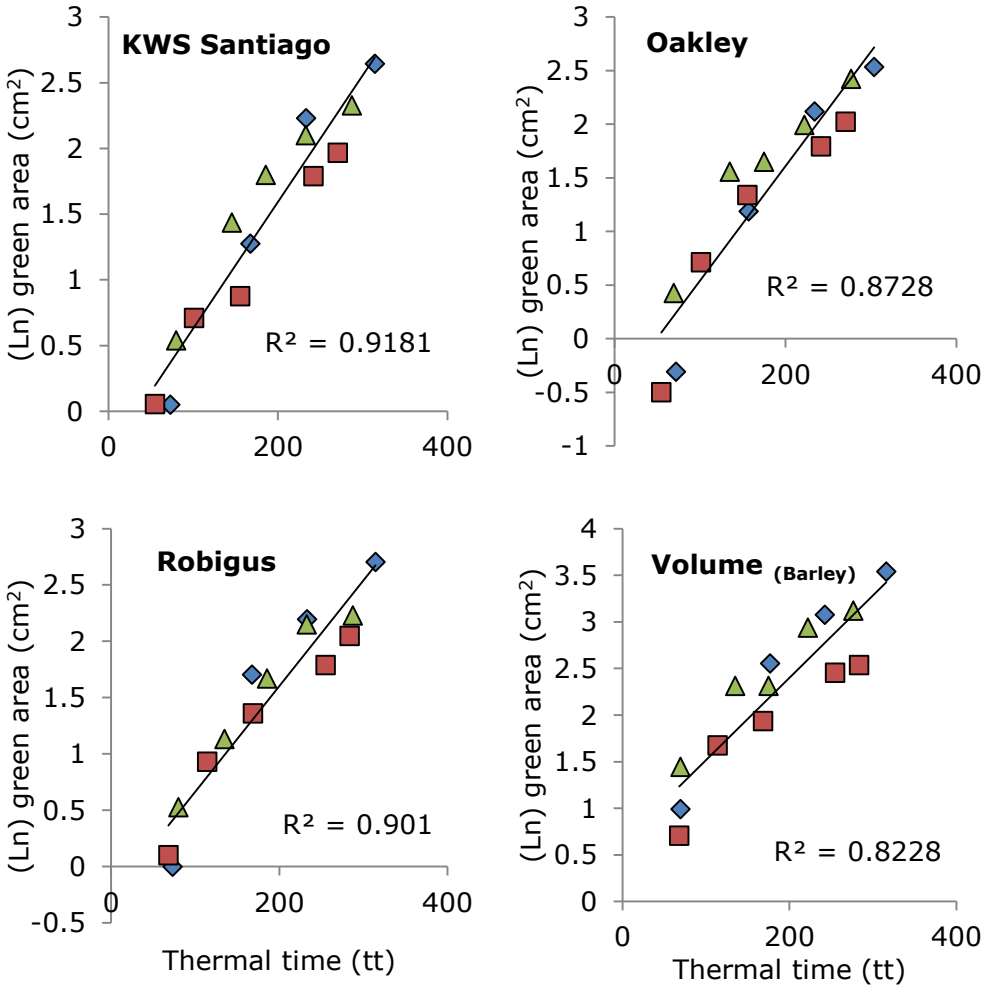

Figure 2.3b - Cultivar green area during autumn. ◆ = 2011, ■ = 2012, ▲ = 2013.

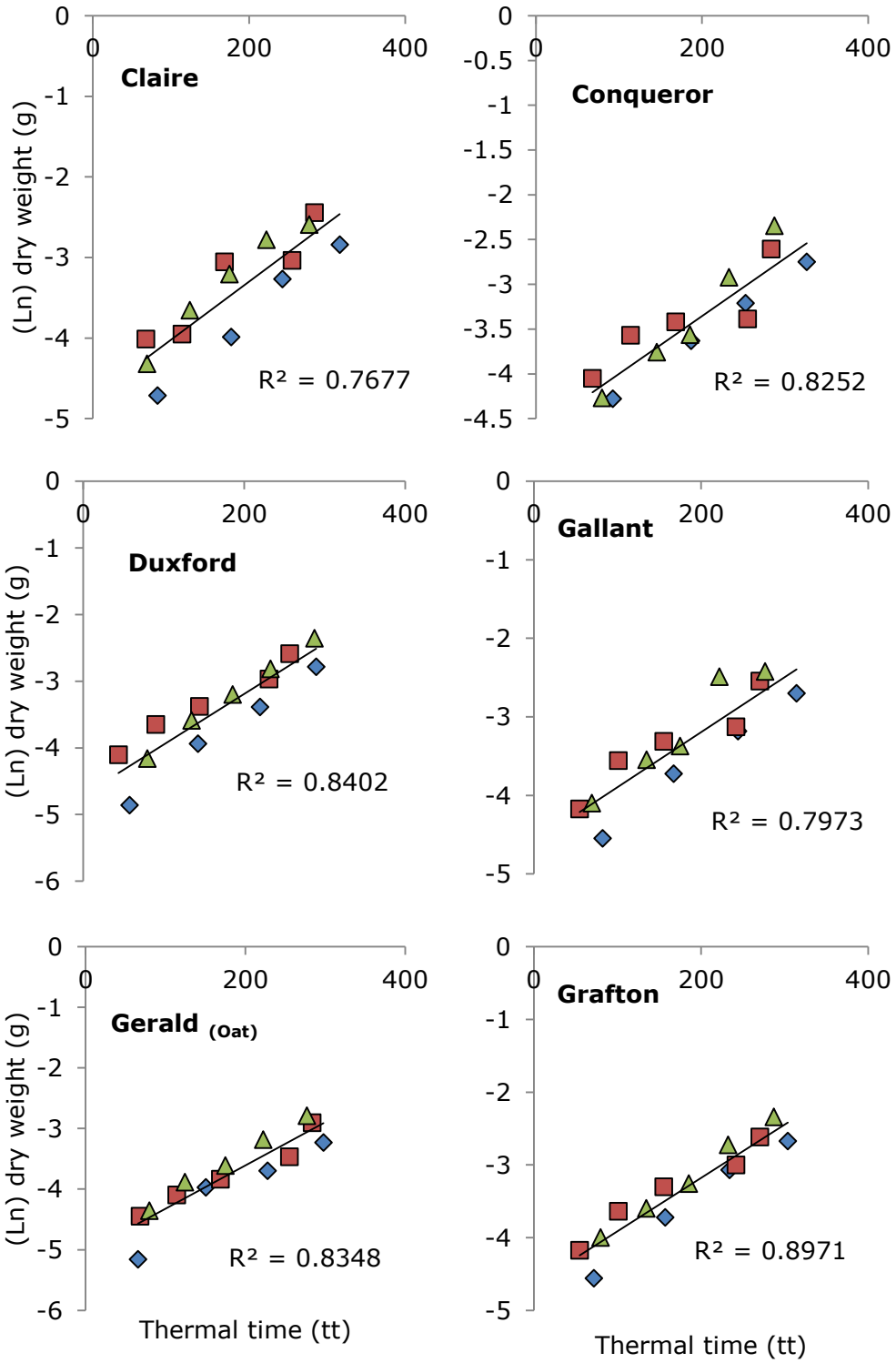

Figure 2.4a - Cultivar dry weight during autumn. ◆ = 2011, ■ = 2012, ▲ = 2013.

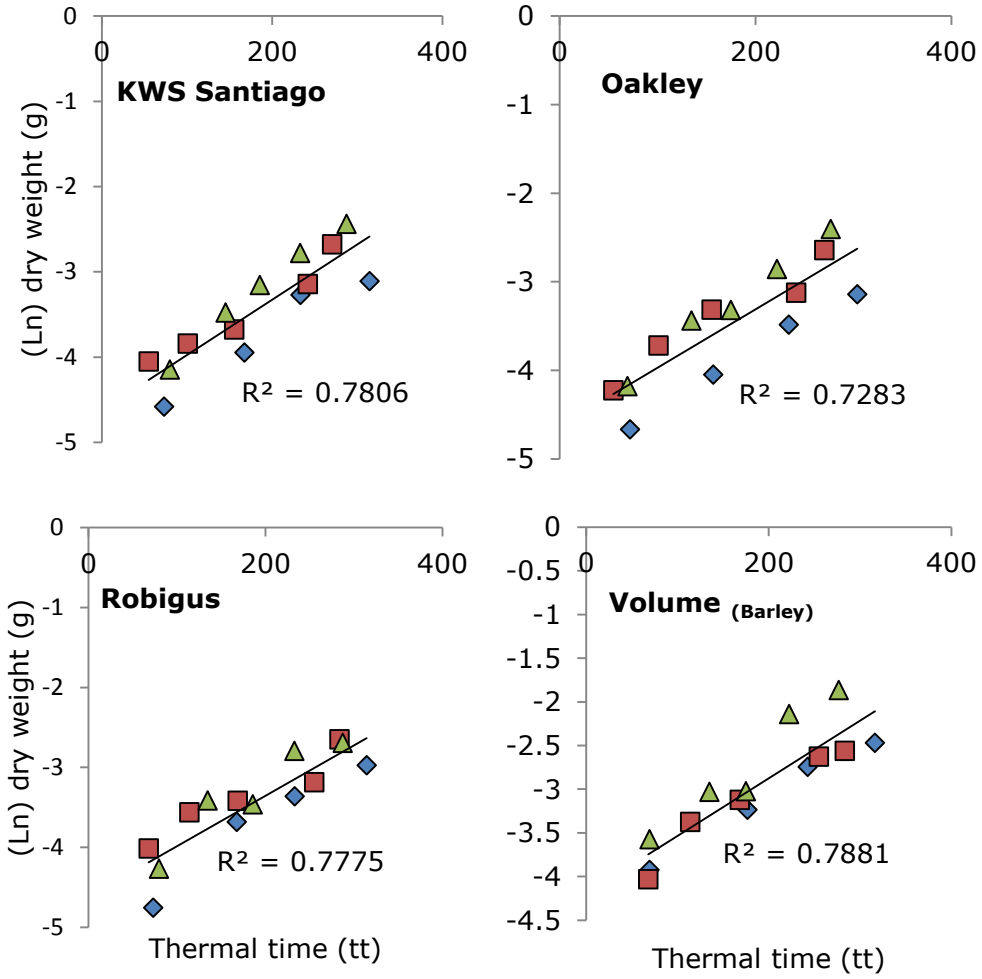

Figure 2.4b - Cultivar dry weight during autumn. –◆ = 2011, ■ = 2012, ▲= 2013

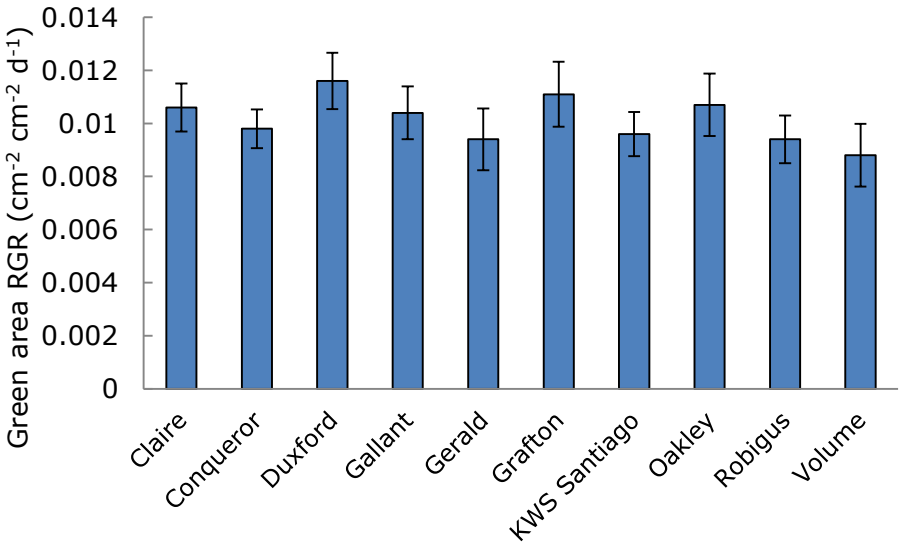

Figure 2.5 – The mean predicted RGR_{GA} of cultivars, with standard errors. All cultivars are wheat, except Gerald (oat) and Volume (barley)

2.4.2 Performance of the relative green area model

Predictions of yield loss differed between cultivars (Figure 2.6). The strongest competitor was predicted to be Duxford, with the weakest being the oat cultivar, Gerald, reflecting differences in seedling vigour assuming all other things being equal. The ranking of cultivars remained reasonably consistent across seasons. Yield losses predicted by the model varied through the years in response to thermal time between 3 October and 10 January of the years 1990-1999 (Figure 2.7). This is a consequence of the differential response of wheat and *A. myosuroides* to variable temperatures with black-grass benefitting more in warmer years.

Across the 1992/93 and 1994/95 seasons (representing the lowest and highest observed mean daily air temperature, respectively), the differences in accumulation of green area impacted the eventual estimates of L_w. For Duxford, predictions of green area differed by an order of magnitude (Figures 2.8 and 2.9). It could be expected that these yearly differences result in canopy closure occurring at different times. Across all years, cultivars with a higher RGR have greater capacity to decrease L_w through high accumulation of green matter. Although *A. myosuroides* has an RGR_{GA} of 0.0108, higher than any of the cultivars (Table 2.3), it always had a lower predicted green area than the cultivars modelled (Figures 2.8, and 2.9). This can be attributed to lower L_0 values for *A. myosuroides*.

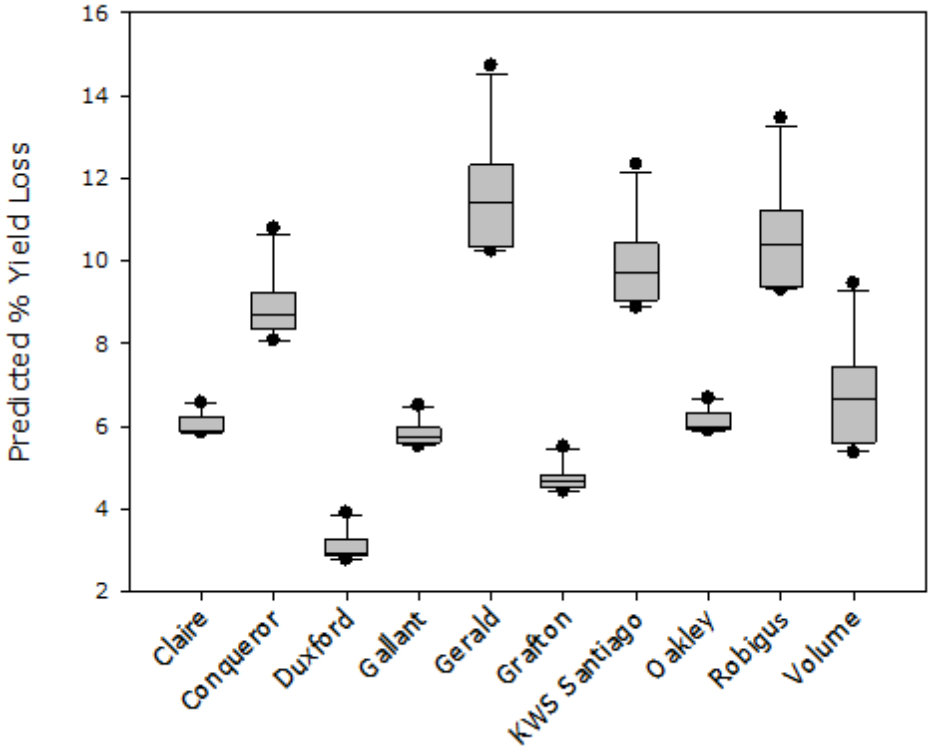

Figure 2.6 - The predicted yield loss (%) for each cultivar for years 1990-1999. All cultivars are wheat except Gerald (oat) and Volume (barley)

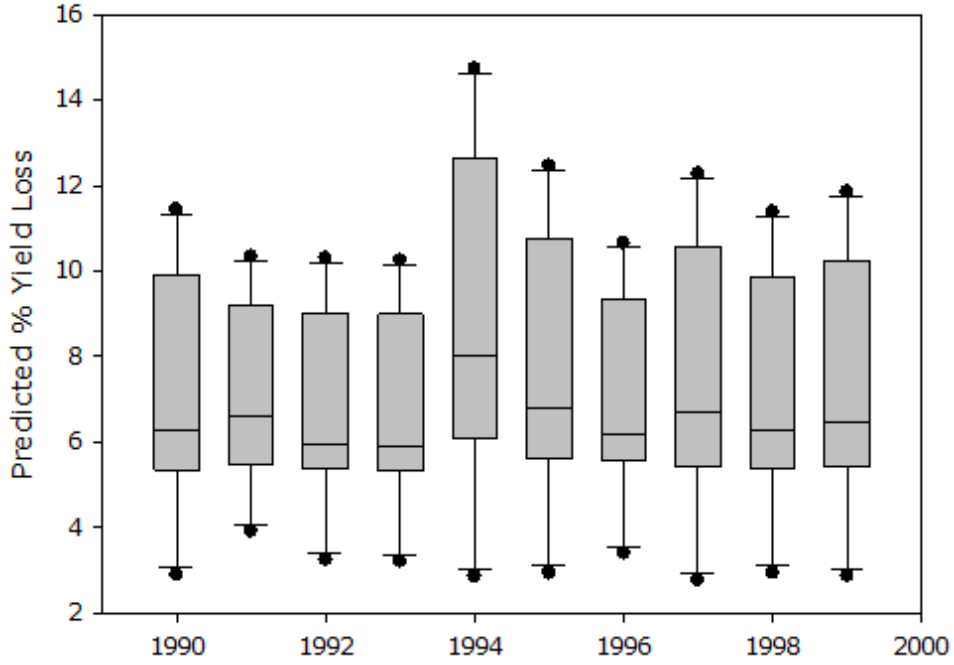

Figure 2.7 - Predicted yield loss (%) during the years 1990-1999. All cultivar values included.

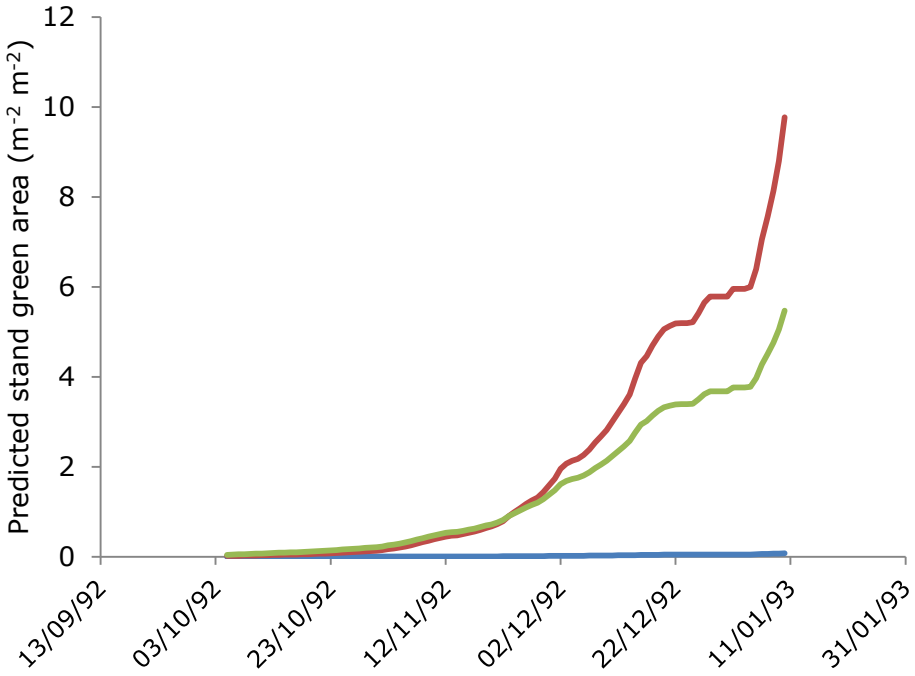

Figure 2.8 - The predicted green area growth of *A. myosuroides* and the highest (Duxford) and lowest (Volume) RGR-ranked cultivars, according to 1992/93 thermal time data (average air temperature 5.68°C). Cultivar density 186 m^{-2}, *A. myosuroides* density 20 m^{-2}. Blue = *A. myosuroides*; Red = Duxford; Green = Volume.

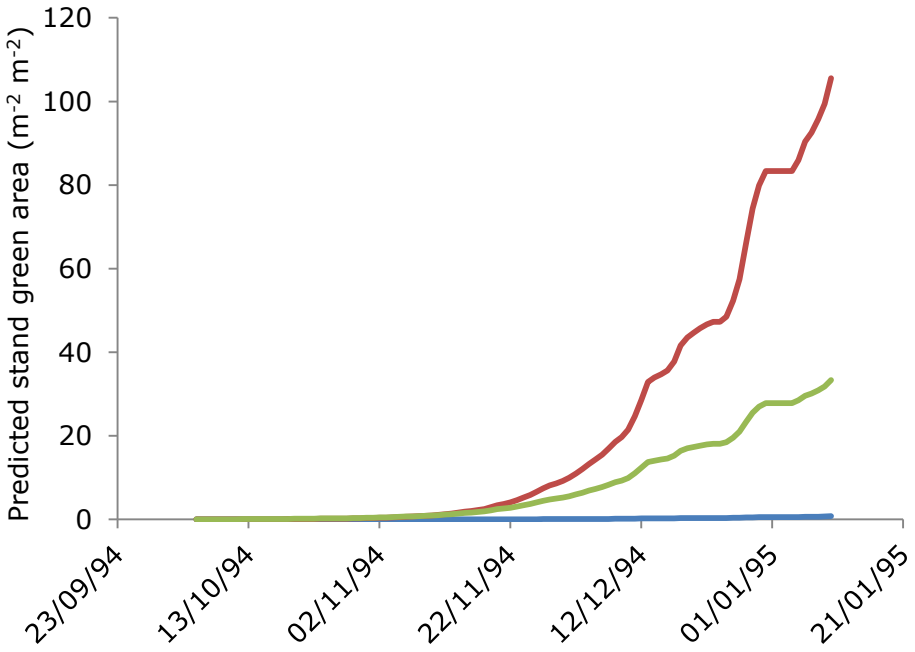

Figure 2.9 - The predicted green area growth of *A. myosuroides* and the highest (Duxford) and lowest (Volume) RGR-ranked cultivars, according to 1994/5 thermal time data (average air temperture 8°C). Cultivar density 186 m^{-2}, *A. myosuroides* density 20 m^{-2}. Blue = *A. myosuroides*; Red = Duxford; Green = Volume.

2.4.3 Traits and trait relationships

The barley (Volume) and oat (Gerald) trait values differed from those observed in the wheat cultivars (Table 2.4). Volume had higher L_0, SLA, LWR and LAR than wheat and oats. It also had the lowest observed RWR and NAR of all cultivars examined. Gerald typically varied in traits, though not so dramatically, with the second highest LAR, joint-highest LWR (with Volume), joint-lowest RWR and lowest W_0. Given that the barley and oats cultivars were the sole examples of their species, generalisations about the species cannot be drawn with confidence. However, in the first year of study, where three barley cultivars were included, all three typically occupied the same ranked positions for the aforementioned traits (data not shown).

The difference between species was considered when producing the correlations matrix, as the extremes of these species could be drivers for correlations between traits. Many of the correlations observed when all cultivars were assessed together (Table 2.5) disappeared and decline of the strength in the 'wheat-only' analysis (Table 2.6). This suggests that the barley and oat cultivar were, in some cases, drivers for trait correlations.

Only NAR in the 'all-cultivars' analysis was significantly correlated with RGR_{GA} (Table 2.5). The positive relationship was in agreement with that seen in the literature (Shipley, 2002; Shipley, 2006). Both analyses returned a negative correlation between NAR and LAR. The negative correlation was also observed between NAR and LARs components, SLA and LWR ('all-cultivars' only), suggesting an interaction between these two components of RGR. The lack of other anticipated trait

relationships could be due to a limited pool size, and/or the similarity of the wheat cultivars.

Table 2.4 - The mean ecophysiological trait values for each cultivar. Mean derived from the experiments run in the autumns of 2011, 2012 and 2013.

Cultivar	RGR_W (g^{-1} g^{-1} tt^{-1})	RGR_{GA} (cm^{-2} cm^{-2} tt^{-1})	NAR (gm^{-2} tt^{-1})	LAR (cm^2 g^{-1})	SLA (m^2 g^{-1})	LWR	RWR	W_0 (g)	L_0 (cm^2)
Claire	0.0072	0.0106	0.70	138.11	0.041	0.36	0.35	0.0087	0.64
Conqueror	0.0065	0.0098	0.68	139.35	0.037	0.37	0.35	0.0096	0.71
Duxford	0.0076	0.0116	0.70	149.97	0.039	0.38	0.31	0.0090	0.67
Gallant	0.007	0.0104	0.68	137.78	0.037	0.37	0.33	0.0101	0.76
Gerald (oat)	0.0071	0.0094	0.65	157.33	0.038	0.42	0.26	0.0065	0.68
Grafton	0.0073	0.0111	0.68	126.52	0.037	0.36	0.35	0.0096	0.60
KWS Santiago	0.0065	0.0096	0.67	130.57	0.035	0.38	0.35	0.0098	0.72
Oakley	0.0066	0.0107	0.80	126.73	0.034	0.37	0.35	0.0098	0.59
Robigus	0.0063	0.0094	0.64	137.78	0.038	0.37	0.35	0.0099	0.76
Volume (barley)	0.0066	0.0088	0.49	188.93	0.044	0.42	0.26	0.0151	1.88

Table 2.5 - Correlation coefficients matrix of RGR and its components. All cultivars included * = P<0.05, ** = P<0.01, *** = P<0.001

	RGR_W	RGR_{GA}	NAR	LAR	SLA	LWR	RWR	L_0
RGR_{GA}	**0.7264***							
NAR	0.2161	**0.6931***						
LAR	-0.001	-0.5325	**-0.8333****					
SLA	0.1808	-0.3155	**-0.7475***	**0.8144****				
LWR	-0.0563	-0.6094	**-0.6715***	**0.8579****	0.4699			
RWR	-0.1702	0.4378	0.6198	**-0.8749*****	-0.5666	**-0.9554*****		
L_0	-0.231	-0.5498	**-0.8739*****	**0.8557****	**0.7039***	**0.6547***	-0.6111	
W_0	-0.0722	-0.0869	-0.5824	0.5858	0.5876	0.274	-0.2557	**0.7892****

Table 2.6 - Correlation coefficients matrix of RGR and its components. Wheat only. * = P<0.05, ** = P<0.01, *** = P<0.001

	RGR_W	RGR_{GA}	NAR	LAR	SLA	LWR	RWR	L_0
RGR_{GA}	**0.9072****							
NAR	-0.033	-0.038						
LAR	-0.2977	-0.3202	**-0.8058***					
SLA	0.0545	-0.0436	**-0.8186***	**0.8572****				
LWR	-0.5349	-0.4382	-0.5004	**0.7417***	0.3079			
RWR	0.5554	0.4808	0.6151	**-0.8613****	-0.4873	**-0.9568*****		
L_0	-0.0445	-0.0905	**-0.7821***	**0.7423***	**0.8335***	0.2332	-0.47	
W_0	0.2867	0.1958	-0.3874	0.0671	0.429	-0.4809	0.2409	0.6733

2.5 Discussion

2.5.1 Relative growth rate and the relative weed green area model

Relative growth rate and initial values at zero *tt* of both dry weights and green area were found to vary amongst the cultivars, and could be described well using thermal time. Green area-based values impact on the final relative weed area index at canopy closure and subsequent cultivar yield loss predictions, and although the impact of temperature in a given year were visible, cultivar differences in RGR_{GA} and L_0 were more important drivers of variance in yield loss due to competition. With the ecological value of RGR in competitive interactions well established in the literature (Grime, 1979; Tilman, 1987), these results suggest that this model can determine the differing ability of the cultivars to resist yield loss across years.

There was evidence of differences in the components of seedling vigour between the three crop species' included in the study. Volume did not observe the highest yield loss, despite having the lowest RGR_{GA}. Its L_0 was approximately three times greater than that of other cultivars, granting it some ability to compensate for the slower rate of growth. As both RGR_{GA} and L_0 capture aspects of seedling vigour, this would support suggestions that use of a single value to represent early vigour (and its involvement in crop competition) could be misleading.

The strength of this type of model is its simplicity to use compared to density-based models once parameters have been acquired. If relative weed green area can be assessed visually (or automatically with image analysis software), predictions can be quickly acquired at the field level when compared to density counts (Storkey *et al.*, 2000), and daily temperature data can

be accessed readily from online sources. A potential weakness of the simple approach used here to assessing the importance of seedling vigour on competitive ability is that a single value for *q* and *m* is used for all cultivars. The parameter *q* value utilised here is as determined for wheat - *A. myosuroides* competition, fixed for making estimations based on relative weed green area being assessed on 10 January (Storkey *et al.*, 2003). As such, the value of 4.2 has been calibrated for the wheat cultivar used in that study, which was not represented within the set of cultivars used here (cv. Mercia). The rationale is that, by assuming all cultivars are equal after the 10 January, the effect of variation in RGR can be isolated. However, it may be argued that to make yield loss estimates more realistic an individual *q* value would be required for each cultivar in this study – and certainly for the different crop species. In terms of the implementation of the model as a decision support tool for farmers this would be impractical, given the number of cultivars and their short duration in the UK markets. How necessary this is would depend on how much the value varied between cultivars, and if a cultivar-based approach were to be adopted the differences in *q* and its subsequent impact on predictions of yield loss should be assessed. This argument is strongest for the cultivars Volume and Gerald, as they represented barley and oats and had lower RGR_{GA} values than the wheat cultivars.

An additional drawback of the approach is that it assumes a uniform density of weeds, which can strongly influence calculations of the economic threshold (Thornton *et al.*, 1990). This may be partially overcome by applying it solely to high weed density patches rather than at the whole-field level. However, early identification of weed patches would make this approach difficult, though with developments in precision

agriculture it may become increasingly feasible (Ali *et al.*, 2013).

Density of the weed and crop is adjustable within the model. This would be expected to impact on the time of canopy closure, should it be used for varying densities. As a result, the *q* parameter would change. A similar difficulty could be expected in warmer years, where a longer period for RGR_{GA} to be possible results in earlier canopy closure. For this model to be applied in agricultural settings, it would be beneficial if this interplay could be accounted for.

It is also suggested that the competitive strength of *A. myosuroides* in wheat, as indicated by the *q* value of 4.2, may mean it is too risky for the model to be used by farmers when determining when control measures are required. Any errors could result in high yield losses (Storkey *et al.*, 2003).

2.5.2 Relationships between RGR and its components

In general, studies into RGR and its components focus on the description of RGR in terms of total biomass, rather than green area. This is highlighted because RGR_{GA} is central to the relative weed green area model and under discussion, not RGR_W. Many of the anticipated relationships between RGR_W and its components were not observed here. However, some were observed in relation to RGR_{GA}.

2.5.2.1 *Components of RGR*

In examining wheat alone, the lack of interaction between RGR_{GA} and its components deviates from what would be anticipated compared with these studies. Only in the 'all-cultivars' analysis did NAR alone correlate with RGR_{GA}. This could be due to the size and nature of the study pool. Classical studies of these trait relationships compare multiple species of

varying life-history strategy. This study takes a primarily within-species approach, and so a smaller range of values would be expected. For example, Poorter and Remkes (1990) studied 24 species, and reported RGR_W ranging from 113 to 365 mg^{-1} g^{-1} d^{-1} and LAR ranging from 12.9 to 35.9 m^2 kg^{-1}. These traits were highly correlated in their study. This in stark contrast to the RGR_W range of 0.0063 to 0.0076 g^{-1} g^{-1} tt^{-1} and LAR range of 126.53 and 188.93 cm^2 g^{-1} reported in this study.

The traits between wheat cultivars often did not differ from one another to the same extent that they differed from Volume (barley) and Gerald (oat). This could explain why correlations with RGR_{GA} were only apparent in the 'all-cultivars' analysis. In the all-cultivars analysis, only NAR was related to RGR_{GA}. As such, the dataset presented does not provide a strong case for the enhancement of RGR_{GA} in cultivars via the selection of any morphological or physiological component. A larger study, including a greater number of cultivars of all three species, may reveal if this is due to the small number of cultivars or if the contribution of components is not readily observable within-species due to low variance.

The relationship between NAR and RGR_{GA}, however, was consistent with observations in the literature. Typically, the single or greatest contribution is made by either LAR (and its components) or NAR. Specific leaf area was most frequently considered the key determinant of RGR (Atkin *et al.*, 1996; Hunt & Cornelissen, 1997). High SLA being negatively associated with leaf lifespan (Poorter & Garnier, 1999), indicating in high leaf turnover and increased light interception per unit biomass. In a study including 24 Western European species a strong correlation was evident between RGR and SLA-driven LAR (and, though weakly positive and non-significant,

NAR) (Poorter & Remkes, 1990). As such, SLA was classically considered the strongest indicator of life history strategy, and has been an important trait in proposed ecological theory (Westoby, 1998).

However, in further research, the contribution of NAR to RGR became more apparent (Shipley, 2000; Shipley, 2002; Shipley, 2006; Storkey, 2004; Fu *et al.*, 2012). In work conducted using 18 UK weed species in outdoor sand-beds, Storkey (2004) found NAR was the strongest determinant of RGR in autumn-sown seedlings, but SLA-driven LAR also contributed in spring-sown seedlings. Under the comparatively low irradiance of controlled experiments, SLA, thus LAR, became the more important contributor to RGR, potentially leading to an overstatement of its importance in determining RGR in earlier studies (Shipley, 2002). Net assimilation rate was the best predictor of RGR in cereal crop progenitors, which was attributed to high irradiance levels (Cunniff *et al.*, 2014). Within species, the contribution of LAR components and NAR been shown to respond plastically depending on light levels (Shipley, 2000).

In this study SLA and LWR were both positively correlated with LAR in both assessments, but none of these traits were significantly linked to RGR_{GA}. This commonly-observed relationship may have been discernible with a higher number of cultivars, though reflects the findings of Storkey (2004) when growing species under similar experimental conditions. This study suggests that promoting RGR for a competitive advantage over *A. myosuroides* would be best accomplished through selection of NAR in breeding programmes.

2.5.2.2 *The LAR-NAR trade-off*

As discussed earlier, the LAR and NAR, and their respective components, rarely seem to promote RGR increase simultaneously. Poorter and Remkes (1990) performed a pathway analysis on RGR, LAR and NAR, and concluded that a negative correlation between LAR and NAR may be responsible, suggesting the presence of a trade-off. This is supported by the results of the current study. Whilst one component may boost RGR, another correspondingly decreases, thus weakening the observed correlation between itself and RGR. Given the importance of RGR for determining the outcome of crop - weed competition, understanding these trade-offs could be an important step in exploiting the potential for increasing cultivar competitiveness through faster early growth.

There are numerous speculations regarding the nature of the negative association between NAR and LAR, and whether NAR is interacting with LWR or SLA. Poorter and Remkes (1990) observed a negative correlation between NAR and LWR, suggesting the cause to be reduced RWR resulting in inadequate water supply limiting photosynthesis. This negative association has also been reported in differing nutrient regimes. Leaf weight ratio positively correlated with RGR in high-nutrient treatments whilst NAR supplanted LWR in low-nutrient treatments (Meziane & Shipley, 1999).

Using data from Poorter and Van der Werf (1998), Shipley (2002) showed that NAR was lower and less variable between species at low irradiance, becoming higher and more variable between species as it increases. Specific leaf area behaves counter to this - at higher light levels SLA become lower and less variable, but becomes higher with greater interspecies variance at low light levels. It was proposed that an SLA-NAR

trade-off permits flexibility to maximise RGR under different light conditions. Other studies support this theory (Hunt & Cornelissen, 1997; Cunniff *et al.*, 2014). A trade-off between SLA and NAR is also suggested under exposure to sub-optimal air temperatures (Loveys *et al.*, 2002; Medek *et al.*, 2007).

A statistically significant negative correlation between SLA and NAR was observed in both analyses of this study, which may be explained by the mechanism proposed by Shipley (2002). But it is noteworthy that a negative association between LWR and NAR is evident in both analyses, and is statistically significant in the 'all-cultivars' analysis. This may suggest that both trade-offs are relevant to the cultivars under study, though a potential NAR-LWR interaction is only evident between species. It is of interest that NAR-SLA negative relationship was visible between cultivars of the same species, implying its greater importance between wheat genotypes. But due to a lack of LAR-component relationship to RGR_{GA} that was statistically significant, NAR remains the trait of primary interest in attempts to boost competitive ability in breeding programmes.

2.5.2.3 *Relating findings to the field*

It is important to remember that many studies characterising associations between RGR and other traits are conducted under near-optimal conditions. Although it is a logical decision in order to control confounding variables, findings from these studies must be applied to field conditions with caution, as resources and conditions are most frequently sub-optimal (Shipley, 2006). For example, SLA, though often related to RGR in controlled environment studies, is a very plastic trait in natural settings (Wilson *et al.*, 1999). Though the findings of this study are likely a better representation of what would be observed in-

field, caution should be exercised when relating its findings to controlled experiments.

While the study described herein was conducted outdoors, it does not directly represent the conditions that cultivars would be exposed to in the field. Exposure to wind likely differed and a regular watering regime was in place. Nutrient availability can impact the LWR-NAR relationship, as reported in 22 species grown in the first 35 days of growth (Meziane & Shipley, 1999). The physical structure of the soil is unlikely to reflect that of the field, as it will not have been broken and prepared for sowing, resulting in root restriction.

The methodology used, however, represents an improvement on near-optimal conditions found in controlled environment studies whilst providing an experimental design that could undergo statistical analysis. The cultivars were exposed to natural day length, and to air temperatures similar to field conditions that were appropriately accounted for by the use of thermal time. As such, the estimations made here could be considered an appropriate improvement.

2.6 **Conclusion**

The relative weed green area model demonstrates an application of the ecological value of RGR in competitive theory to an agricultural setting. The only observable driver behind RGR_{GA} was NAR, and was driven by the inclusion of the single barley (Volume) and oat (Gerald) cultivars. Whether it is possible to boost the RGR_{GA} between cultivars of the same species is uncertain, though a larger study pool may reveal more. This study suggests that NAR is the functional trait of greatest value in any attempts to boost the RGR_{GA} of cereal

cultivars, which is worth consideration in any attempts to boost RGR_{GA} through breeding efforts.

There is potential for the RWGA approach to be employed in making weed control management decisions. This is owing to differences in RGR_{GA} and L_0 between cultivars that had consistency over multiple years. Predicted yield loss for cultivars saw little variation across the 10 years in which predictions were ran. Developments in capturing green area index may make this approach more feasible in field. However, caution would be required in using this relatively simple model at field level, as incorrect predictions could lead to high yield losses.

3 Chapter three – The traits that govern the suppressive ability of cultivars: results from container experiments.

3.1 Introduction

Suppressive ability is the capacity of a species to reduce the fitness of another species through competition for limited resources. Cereal cultivars have been observed to differ in their suppressive ability for many decades (Wicks *et al.*, 1986; Lemerle *et al.*, 1996).

However, suppressive cultivars have seen limited adoption in commercial agriculture. Reliable predictions of a cultivar's suppressive ability need to be available at the time of their commercialisation, as well as advice on how to best make use of them (Cousens & Fletcher, 1990). An understanding of the traits that contribute to the ability to suppress weeds, and how these traits interact with the environment, may lead to a protocol to predict the suppressive ability of cultivars (Hansen *et al.*, 2008; Seavers & Wright, 1999).

Often a trait is reported as being suppressive in one study, but not observed in another. In multiyear and locational studies, this lack of consistency and predictability is often observed (Cosser *et al.*, 1997; Huel & Hucl, 1996; Coleman *et al.*, 2001; Roberts *et al.*, 2001; Vandeleur & Gill, 2004). The interaction of traits with environmental conditions, such as rainfall and temperature, may drive this variability (Seavers & Wright, 1999). As such, it is widely accepted that competitive ability cannot be linked to a sole trait (Moss, 1985; Lemerle *et al.*, 2001; Roberts *et al.*, 2001; Mennan & Zandstra, 2005; Watson *et al.*, 2006). This strengthens the need for a multi-trait

approach in predicting the competitive ability of a cultivar (Christensen, 1995; Mennan & Zandstra, 2005).

This chapter will focus on the ability of cultivars, and their traits, to suppress the seed production of *A. myosuroides*. The experiment was conducted in containers on outdoor sand-beds. The results of an equivalent experiment, conducted in the field, will be presented in Chapter Four. Whilst the in-field experiment will more closely reflect the outcomes of competition in equivalent commercial crops, the container study presented within this chapter allowed for greater control of extraneous variation and ease of data collection. The results of both chapters will be compared in the general discussion.

3.2 Aims

In this chapter, the following hypotheses will be tested:

1. The ranking of the suppressive ability of cultivars, measured in terms of *A. myosuroides* seed return, will be consistent over the three years of study.
2. Plant traits will be associated with a cultivar's suppressive ability over *A. myosuroides* in containers replicating field conditions.
3. The traits related to cultivar suppressive ability will be consistently expressed in different environmental conditions.

3.3 Materials and methods

3.3.1 Cultivar choice and seed sourcing

Nineteen cultivars were included in the experiments conducted during the 2011-12 growing season. In the 2012-13 and 2013-14 growing season, the number of cultivars was reduced to 12. This was to include additional experimental conditions, to

observe how these influenced competitive outcomes (discussed in Chapter Five). Details on cultivars included in the study can be found in section 2.3.1.1.

Wheat, barley and oat have been noted to vary from one another in their suppressive ability, with oat being the most suppressive and wheat the least (Seavers & Wright, 1999). It was infeasible to achieve the same desired assessment of barley and oat cultivars due to time and space constraints, and these species were underrepresented in the 2011-12 experiment. As such, wheat became the focus of the experiment, and the potential of oat and barley cultivars to drive the analyses resulted in exclusion from analyses, unless otherwise stated.

The model weed for the suppression studies was *A. myosuroides*. Seeds in the 2011-12 experiment came from collections taken from the Broadbalk experiment at Rothamsted Research, Hertfordshire, UK in July 2009. In the following seasons, *A. myosuroides* seed was sourced from Herbiseed UK. All seed was stored in a controlled environment room at 18 °C and 65-70% humidity.

3.3.2 Experimental set-up

Containers were filled with Kettering loam mixture (80% sterilized screened loam, 20% lime-free grit and 2kg m^{-3} of slow-release Osmocote ® mini slow-release fertiliser) and bases lined with 4 l of Hydroleca to assist drainage. The containers were arranged on the sand-beds at Rothamsted Research, Hertfordshire, UK. The sand-beds were in a netted tunnel, protected from animal damage whilst exposed to all weather conditions, and with supplementary watering during dry periods. There were three replicates of each cultivar, and these were arranged in fully randomised blocks. The experiment

included containers that were sown with seeds to act as spares that may be transplanted into experimental containers should individuals fail to establish.

Alopecurus myosuroides seeds were germinated in petri dishes lined with three Whatman filter papers and soaked in 5.5ml of water with 2 g^{-1} l^{-1} of potassium nitrate. To promote germination, these were placed in an environmental control cabinet under a 14 hr / 10 hr light/dark regime with temperatures at 17°C and 11°C, respectively, for nine to 14 days.

Crop seeds were planted at 20mm depth in a pattern to replicate the standard drill pattern in the field (Figure 3.1 and 3.2). Pre-germinated *A. myosuroides* seedlings with no more than ~5 mm radicle growth were selected and were planted systematically in each container. They were planted by making a small groove and brushing soil on top of the germinated seed with the young root pointed down.

Five individuals were planted within the rows whilst five were planted between the rows. This arrangement was chosen to examine the differences in the seed return of *A. myosuroides* when grown at different proximity to the crop. However, in the 2011-12 season, separating seed return by individual was time-consuming, and provided no evidence of differences with proximity. As a result, data was analysed at the container level, and the planting arrangements were maintained in subsequent years for consistency.

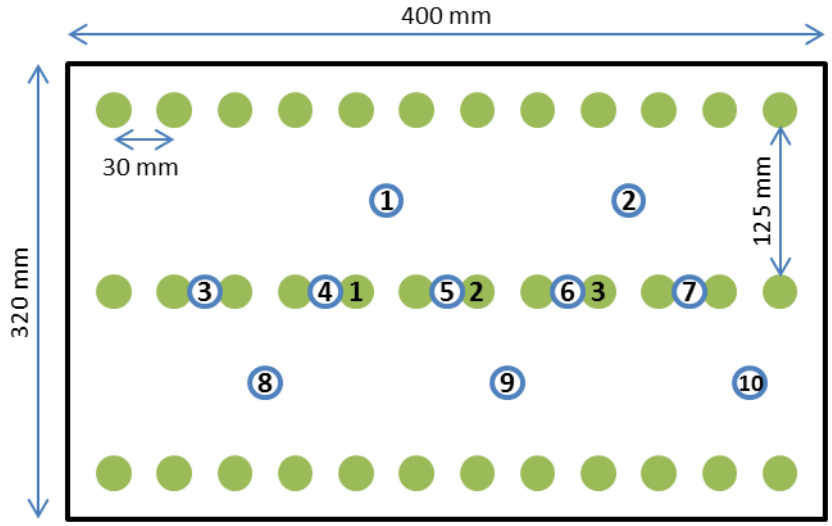

Figure 3.1 - Arrangement of species within containers in the 2011-12 experiment, with sampled individuals numbered. • are cultivars, o are *A. myosuroides*.

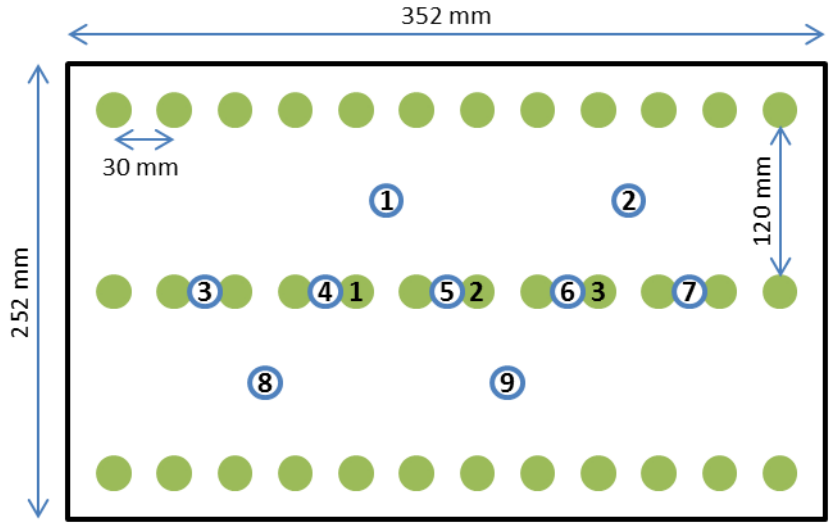

Figure 3.2- Arrangement of species within containers in the 2012-13 and 2013-14 experiments, with sampled individuals numbered. • are cultivars, o are *A. myosuroides*.

In the first year (2011-12), containers were used with the internal dimensions 320 x 400 x 160 mm (Figure 3.1 and 3.3). Damage to the containers required their replacement for further suppression experiments. The closest equivalent dimensions that could be sourced were internal dimensions 257 x 356 x 162 mm, and these were used in the experiments of 2012-13 and

2013-14. Additionally, the number of individual weeds per container was reduced from ten to nine in response to individual ten benefitting from an edge effect, thus escaping a portion of the competition for light (Figure 3.2). Table 3.1 provides a synopsis of the changes between experiments.

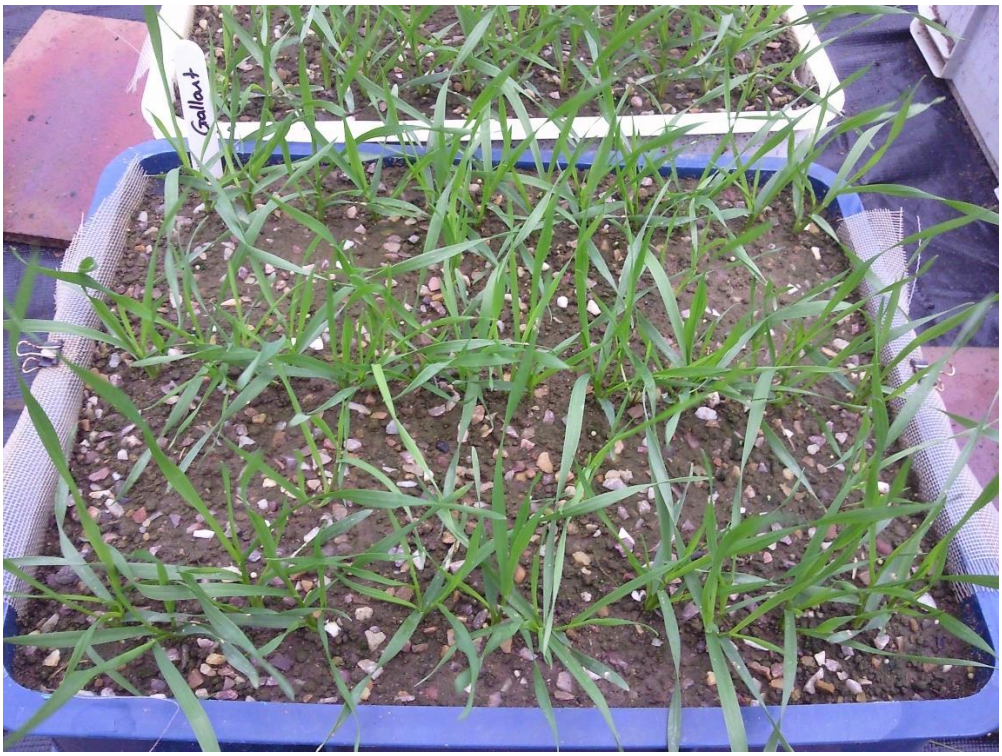

Figure 3.3 – Experimental containers, based on the sand-beds. Cultivars are rows at 12 cm distance and *A. myosuroides* sown within and between rows.

Table 3.1 – Experimental details of the sand-beds suppression experiment

Year	Container dimensions (mm)	Crop density (by field equivalent) (m^{-2})	Crop density (by container) (m^{-2})	Weed density (by container) (m^{-2})	Sowing dates
2011-12	320 x 400 x 160	276.39	281.25	71.4	11-13 Oct 2011
2012-13	257 x 356 x 162	276.39	393.48	98.4	15-17 Oct 2012
2013-14	257 x 356 x 162	276.39	393.48	98.4	14-15 Oct 2013

3.3.3 Data collection

Traits for study were selected after a review of the literature (Chapter One), and further narrowed down after consideration of the time and resource availability.

3.3.3.1 *Emergence*

Every 2-3 days emerged individuals were counted until each cultivar attained ~90% emergence. Percentage emergence was plotted against time in order to determine when each cultivar reached 50% emergence.

3.3.3.2 *Stem counts and height measurements*

All weed individuals and three crop individuals were identified for measurement throughout the study and numbered (as detailed in Figures 3.1 and 3.2). In 2011-12, the tenth *A. myosuroides* individual was excluded from stem measurements when it became apparent that it was benefiting from an edge effect. The individual was excluded from further experiments (see Figures 3.1 and 3.2).

Cultivar height was measured weekly in 2011-12, and biweekly in the following years (with the exception of the stem extension phase, where measurements were taken approximately weekly). Plant height was measured from the soil to the highest point (without artificial interference) using a ruler (Cornelissen *et al.*, 2003).

During the 2011-12 experiment, stem counts were conducted on *A. myosuroides* and cultivars on a weekly basis, and biweekly in the following years. In 2011-12, stem counts were concluded on 24 March 2012, and height counts concluded on 10 June 2012. In 2012-13, both were concluded on 4 July 2013. Stem counts were extended in the second and third year, as it

became apparent that stem loss was occurring during stem extension.

3.3.3.3 *Early growth form and leaf parameters*

The length and width of leaves were measured for 2012-13 and 2013-14 experiments on 18 March 2013 and 3 Dec 2013. Dates of sampling differed due to time constraints.

Leaf counts were conducted until 22 December 2011 (weekly measurements), 28 January 2013 (biweekly), and once in the 2013-14 experiment (27 November). Angle of leaves one and two were measured on 4 December 2012 and 27 November 2013, when the cultivars were at approximate growth stage 13 using a protractor. The cross-point was positioned where the leaf left the stem, and the base of the protractor held parallel to the ground. Angle was measured in relation to how far it deviated from the upright position (0°); leaf angle is greater for more prostrate cultivars.

3.3.3.4 *Spike emergence*

Spike emergence may be used as a measure of plant maturity. In 2012-13 and 2013-14, emerging spike counts were conducted on a 2-3 day basis. Any spike with visible peduncle was included in counts until no further spikes emerged (Mason *et al.*, 2008). From this, percentage spike emergence was quantified for each data and plotted against time, to derive the date at which 75% spike emergence was reached.

3.3.3.5 *Weed fitness*

Alopecurus myosuroides seed heads were collected between 7 and 14 June 2012, 17 and 21 June 2013, and 28 May and 4 June 2014, as the seeds began to ripen. Collected seed heads were stored in a drying room. When they were deemed suitably dry, three seed heads that had not shed any seed were

randomly selected from each replicate. The seed head length was measured (Figure 3.4) and the seeds removed and counted, so that a mean number of seeds per mm could be calculated across all samples. The total length of seed heads was measured and multiplied by seed per mm to obtain an approximate total seed return for each container. Due to time constraints, in the third year a subsample of 50 seed heads from each sample was measured for length, then dried and weighed separately to the remaining seed heads to gain an estimate of total length of seed heads.

Figure 3.4 – The measurement of *A. myosuroides* seed head lengths, in order to calculate seed return in each container.

Alopecurus myosuroides plants were harvested between 6 and 12 July 2012, 15 and 18 July 2013, and 22 and 23 July 2014. Working from replicate one to three, they were cut from the soil level and placed in one bag per replicate for each cultivar. Weed material (including seed heads previously collected) was dried

at 80°C for at least an 18 hr period. Once dried, the plant matter was weighed to one decimal place.

3.3.3.6 *Flag leaf measurements*

At the same time as harvesting *A. myosuroides* biomass, 10 cultivar flag leaves were gathered from each sample. These were selected at random by blindly gripping a stem and removing its flag leaf (if it possessed a flowering head). In 2011-12, this was not possible for barley cultivars as the plants were damaged by rodents. The width and length of the flag leaves were measured using a ruler. In 2013-14 specific leaf area was quantified by measuring area and weighing the leaves after drying at 80°C overnight. The WinDIAS software was used to measure leaf area, by capturing leaf area through use of a light projector followed by calculation of area in the pre-calibrated programme.

Flag leaf angle was measured on 12 July 2013 and 5 June 2014. The cross-point was positioned where the leaf left the stem, with the 90° point aligned with the emerged ear. Angle was measured in relation to how far it deviated from the upright position (0°).

3.3.3.7 *Thousand grain weight (TGW)*

One thousand grains of seed sourced for the experiment were counted using an electronic grain counter and dried at 105°C for 18 hr. These were weighed on a one decimal point balance in 2011 and a three point balance in 2012 and 2013, depending on availability of balances. Three replicates for all cultivars were carried out, except Maris Widgeon, for which only two replicates of dry weight were conducted due to limited seed being available.

3.3.4 Fungicide/nutrient programmes

The nitrogen levels in the soil were boosted by the addition of Nitro-chalk™, a fertiliser containing 27% calcium carbonate and ammonium nitrate. It was applied in the spring by evenly scattering across containers to compensate for the depletion of pre-added fertilizer prior to stem extension (Table 3.2). In 2012-13, the quality of the soil varied largely, resulting in the crop visibly suffering nitrogen deficiency of varying extent across the experiment. As such, the quantity of Nitro-chalk applied this year was increased. In the 2013-14 experiment, nitrogen deficiency could be observed in early March, and so the dose was split across two dates – one to tackle immediate deficiencies and one during stem extension.

To limit the impacts of fungal disease, a robust fungicide program was developed for this project on advice from Bill Clarke (NIAB-TAG) and Jason Tatnell (Syngenta UK) (see appendices). No T3 treatment was applied, as the experiment was completed in early July.

Table 3.2 - Applications of Nitro-chalk™ in the sand-bed based suppression experiment

Year of study	Application dates	Quantity per container	Field equivalent (per m^2)
2011-12	17 April 2012	4.75g	37g m^{-1}
2012-13	1 March and 20 May 2013	4.75g (x2)	52g m^{-1} (x2)
2013-14	11 March and 12 April 2013	2.25g (x2)	24g m^{-1} (x2)

3.3.5 Statistical analysis

3.3.5.1 *Time units*

The development of cereals is determined by both temperature and day length. As such, photothermal time (ptt) was

calculated. Photothermal time is a measure that includes thermal time and photoperiod, expressed in equation 3.1.

$$\text{ptt} = \Sigma\left((T_i - T_b) \times \left((P_i - P_b)/24\right)\right) \quad (3.1)$$

Where T_i is the mean daily temperature on day i, T_b is the base temperature, Pi is the photoperiod on day i and P_b is the base photoperiod. Base temperature and base photoperiod were both assumed to be zero.

3.3.5.2 *Suppressive ability of cultivars*

A two-way factorial ANOVA with a Bonferroni multiple comparisons test was applied to *A. myosuroides* seed return per plant when grown alongside cultivars across the three years using cultivar and year as factors. Only cultivars that were present across all three years were included in the ANOVA. Seed return per plant was normalised via logarithmic transformation prior to analysis.

The suppressive ability of individual cultivar traits was examined with Pearson's correlation with *A. myosuroides* seed production. Data from each year was assessed individually.

3.3.5.3 *Modelling growth*

The regular measurement of cultivar height allowed for standard curves to be fitted. From these, various parameters that are potentially relevant to competitive outcomes and related to a biological trait could be extracted.

Cultivar height was measured from three individual plants within each container (see Figure 3.1 and 3.2). As each container represents a replicate, the individual plants must be treated as pseudo-replicates. Additionally, the data represent repeated measures, because the same plant individuals were measured and height at one time-point is partially dependent

on height at a previous time point. The values per pseudo-replicate and the replicate means were included in modelling efforts, as this would allow the mean parameters for each replicate container can be weighted by the goodness-of-fit of the curves. Deriving parameters from the mean values partially accounts for the problems arising from the use of repeated measures.

Height growth was observed to follow a sigmoidal trend. Following consultation with Suzanne Clark (Rothamsted Research), code was generated to simultaneously run constrained and unconstrained logistic, generalized logistic and Gompertz standard curves in Genstat 16. This allowed for careful examination of the fits of all options. It was decided that the unconstrained generalized logistic model provided the best fit of data at the right-hand end of the data, where the parameters of interest would be extracted. The generalized logistic curve may be expressed as:

$$y = a + \frac{c}{(1 + t\exp(-b(x-m)))^{\left(\frac{1}{t}\right)}} \qquad (3.2)$$

Parameters of interest were *a* + *c*, which denotes the upper asymptote (height at maturity), *t* describes the asymmetry of the curve along the y axis, and *m* is the point in photothermal time where the point of inflexion occurs (just prior to reaching the asymptote). This is also the point in time that the slope is the steepest, and so will be described as the time of maximum growth rate. The coding extracted the value of the cultivar's maximum growth rate in accordance with the following equations.

First derivative:
$$\frac{dy}{dx} = \frac{bc\exp(-b(x-m))}{(1+t\exp(-b(x-m)))^{\left(\frac{1}{t}+1\right)}} \quad (3.3)$$

Maximised when $x = m$:
$$\max\left(\frac{dy}{dx}\right) = \frac{bc}{(1+t)^{\left(\frac{1}{t}+1\right)}} \quad (3.4)$$

Heights from an approximate 120 ptt point were selected for use as a measure of early cultivar height. These were taken on 11 November 2011 (119.45 ptt), 3 December 2012 (120.56 ptt) and 27 November 2013 (126.99 ptt). Photothermal time points were used as markers of early height, as development rate is partly determined by both temperature and photoperiod. As such, a similar photothermal time would represent the similar developmental stage across all experiments. If early height were to be used as a predictive trait, this photothermal time point could be associated with a particular growth stage for ease of assessment (approximately GS 13 – the stage at which three leaves have unfolded). This provides a clear assessment time, should a measure of early height be deemed valuable in ascertaining the suppressive strength of cultivars.

3.3.5.4 *Modelling tiller production and loss*

Stem production and subsequent loss has not been rigorously investigated in the context of crop-weed competition. Models were employed to acquire measures of tillering rate, maximum stem counts, % stem loss and final stem number.

Stem number was recorded as counts, which presents difficulties when applying growth models. As such, values were taken by replicate rather than by pseudo-replicate, producing mean values that more closely resembled continuous data.

Owing to the near-linear nature of stem production and loss, a split-line regression model was employed to extract parameters of interest. The split-line model employs two linear regressions that will meet at the highest Y value (termed the 'breakpoint'). Derived parameters were the rate of tillering during stem production (slope 1), the highest recorded stem number (breakpoint Y), and the time point at which highest tiller number was achieved (breakpoint X).

Final stem number could not be reliably derived from this model. As such, the last observed final stem count was included in further analysis, though treated with caution when interpreting output. Stem loss was calculated from breakpoint Y and final observed stem count.

3.3.5.5 *Partial redundancy analysis*

Partial redundancy analysis (RDA), with year as a covariate, was employed to identify traits that are primary drivers of differences between cultivars combining data from all three years. Simple linear correlation analysis can ascertain the relatedness of proposed explanatory and response variables, but inter-correlations may conceal the true relationships between the variables. These are removed by RDA through transformation of explanatory variables into collections of components (axes), each of which accounts for a percentage of variation.

A matrix of traits was assembled and analysed for associations between traits. As traits did not have the same units, the data were standardised to zero mean and unit standard deviation. This was performed by Genstat 16 through submission of data via a correlation matrix, with the ordination plot generated using Canoco. Only data from wheat cultivars were included in

final analyses as differences between species of crop tended to dominate axes one and two, and due to inconsistency in whether the analysis would remove barley and oat cultivars in different years. Cultivar was treated as the explanatory variable, and year was included as a covariate.

The axis scores for cultivars along axes one and two were regressed against *A. myosuroides* seed return per plant, to ascertain if either axis was related to the cultivars suppressive ability. Simple linear regressions were performed for each axis and seed return for the respective year using Genstat 16. If an axis is correlated with seed return, it would suggest that the traits with high loadings could constitute a 'competitive suite', and would be worth further investigation.

3.3.5.6 *Linear mixed model*

Due to the need to account for experimental design, and instances where the design was unbalanced and non-orthogonal, a linear mixed model (LMM) was employed to identify the traits that are the strongest predictors of suppressive ability. Traits of high loading in RDA axis one and correlated to seed return in Pearson's analysis were selected for inclusion in the linear mixed model. The aim was to establish the minimum number that may be included in a model to acquire reasonable predictions of suppressive ability. A linear mixed model was employed using Genstat 16, with block as a random effect and year, traits and traits x year interactions in the fitted model. This model required traits to be entered in order of presumed importance. Order was chosen based on their loadings in the RDA and some consideration of their relationships to seed return in the Pearson's correlation analysis. The order was early height, maximum stem number, time of maximum stem number, LAR, flag leaf length, RGR_W,

time of 75% spike emergence and early leaf width. Seed return was normalised via logarithm to base ten to improve residuals.

The traits LAR and RGR_W were from the ecophysiological traits experiment (Chapter Two) and included in the analysis as a single mean for each replicate. As a result, the same value was present for each cultivar replicate in a year. The LMM examined these traits at the whole treatment level, then seek evidence of lack of fit between the mean of the *A. myosuroides* seed return and the replicates. No evidence of lack of fit was found.

A full model was run, which explored the interaction between years, and terms were sequentially dropped from the model until all remaining terms have significant P-values. The full model dropped 53 of 105 data values from the model, largely owing to traits such as final stem counts not being available in the first year. A full model was additionally run excluding these traits. The results of both models will be presented. Singular trait x year LMMs were also conducted for consideration alongside the full model.

3.4 **Results**

The temperature across the three years differed, and of particular note is the prolonged cold temperatures into the spring of 2013 (Figure 3.5). In 2011-12, the mean daily temperature was 8.3°C, 6.3°C in 2012-13 and 8.9°C in 2013-14. Weekly radiation data for each year is in figure 3.6.

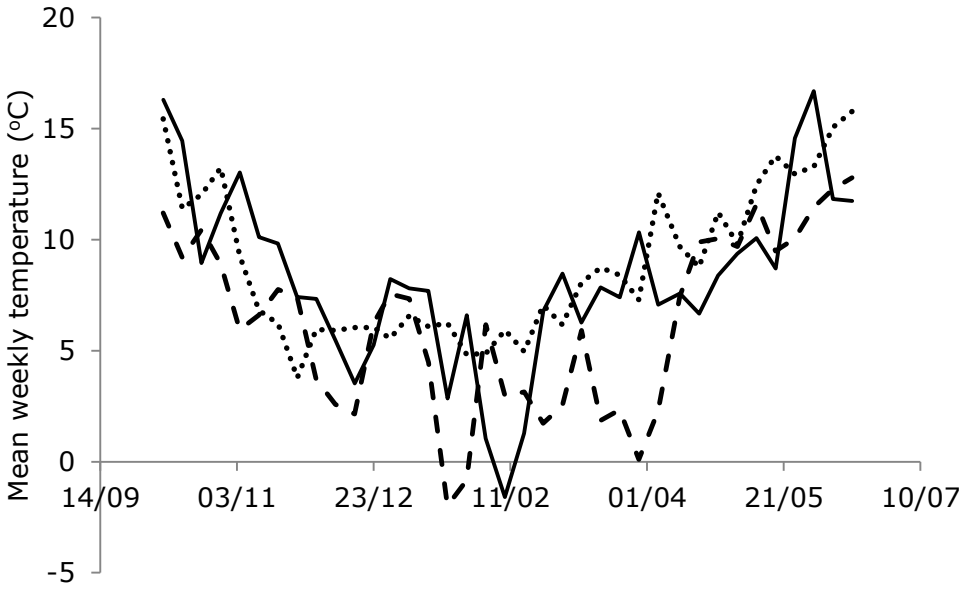

Figure 3.5 - Mean weekly temperatures during experiment at Rothamsted, Herts, UK. Solid line = 2011-12; Dashed line = 2012-13; Dotted line = 2013-14

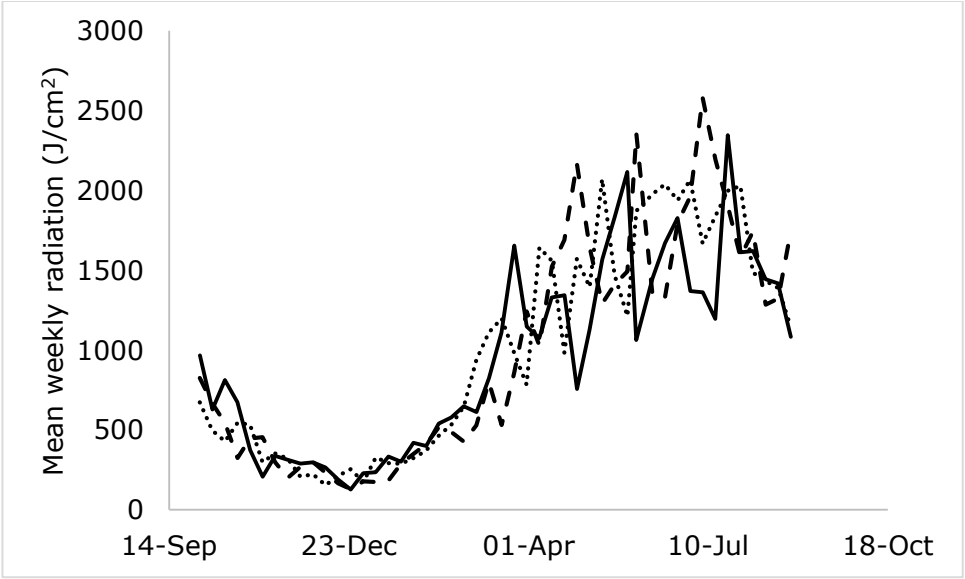

Figure 3.6 – Mean weekly radiation during experiment at Rothamsted, Herts, UK. Solid line = 2011-12; Dashed line = 213-14; Dotted line = 2013-14

3.4.1 Cultivar suppressive ability

The 2-way ANOVA showed that cultivars differed in their ability to suppress the seed production of *A. myosuroides* (d.f. 9; P<0.001), and cultivar suppressive ability interacted with year

(d.f. 18; P<0.001) (Figure 3.7). However, multiple comparisons reveal that differences between wheat cultivars are not significant. Volume, a barley cultivar, was more suppressive than the wheat cultivars. Gerald (oat) was one of the poorest suppressors, though its performance did not differ significantly from the wheat cultivars KWS Santiago, Claire and Grafton.

Limited difference could be observed in cultivar performance in the 2012-13 season. Seed return of *A. myosuroides* in competition with Duxford was lower than KWS Santiago by 35.5% in 2011-12 and 52.2% in 2013-14, but only 20.6% in 2012-13. When 2012-13 was dropped from the analysis, significant differences between wheat cultivar performance could be observed (d.f. 9; P<0.001) and no cultivar x year interaction emerges (Figure 3.8).

Alopecurus myosuroides seed return and dry weight were closely correlated in all three years (Figure 3.9). It was decided to focus on seed return as a measure of fitness.

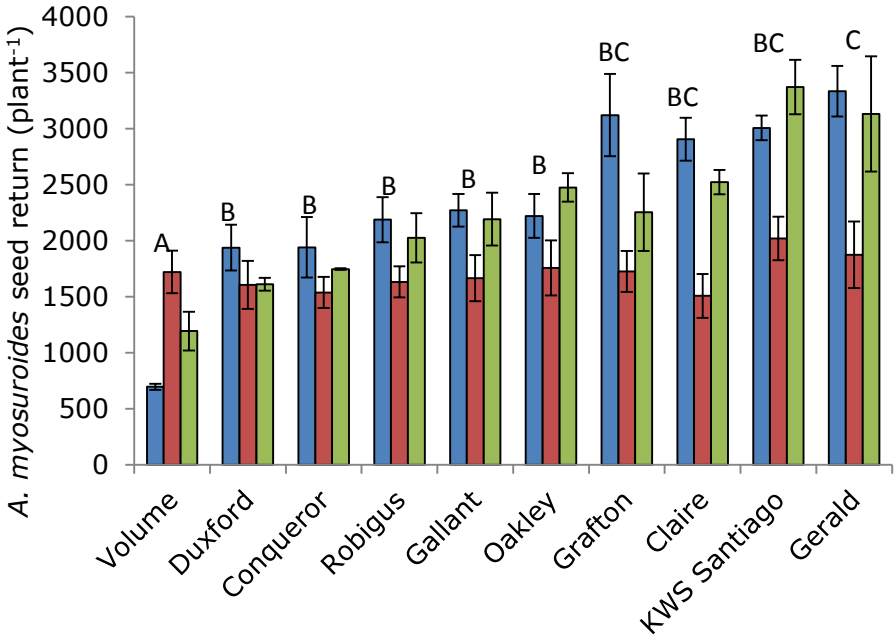

Figure 3.7 - Mean *A. myosuroides* seed return (plant^{-1}) when grown alongside cultivars in different years. All cultivars are wheat, except Volume (barley) and

Gerald (oat). Letters denote Bonferroni significance levels. Bars indicate standard error. ■ = 2011-12; ■ = 2012-13; ■ = 2013-14

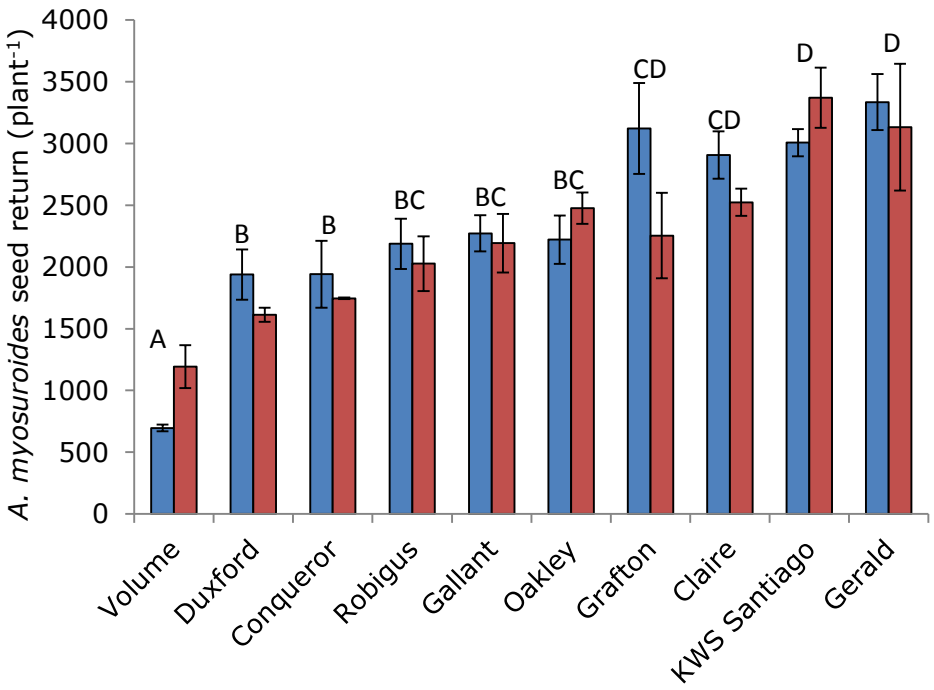

Figure 3.8 - Mean *A. myosuroides* seed return (per plant) when grown alongside cultivars in different years, excluding the atypically cold year of 2012-13. All cultivars are wheat, except Volume (barley) and Gerald (oat). Letters denote Bonferroni significance levels. Bars indicate standard error. ■ = 2011-12; ■ = 2013-14

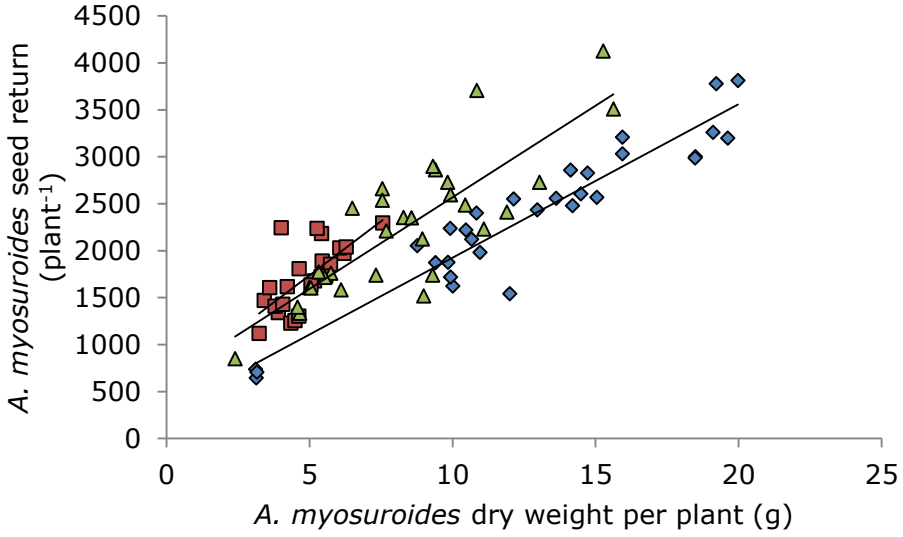

Figure 3.9 - The correlation between *A. myosuroides* seed return and dry weight across three years. 2011-12: r=0.9484;P<0.001, 2012-13: r=0.8216;P<0.001, 2013-14: r=0.8291;P<0.001.

3.4.2 Suppressive traits

The wheat cultivars were the focus of continued evaluation of traits, as barley and oat trait values were frequently far outside the range of those observed in wheat (see appendices) and risked strongly influencing data analyses. Though the Pearson's correlations showed that many traits were related to the suppressive ability to cultivars, often it was only in a single year (Table 3.3). Only LAR was correlated across all three years, whilst early height, early green area and SLA were correlated in two of three years (2011-12 and 2013-14).

The results of the RDA showed that, across all years, traits that separated cultivars along axis one could be defined as early vigour traits (early height, early leaf width and length) (Figure 3.10). The ordination plots indicate that increased early height and leaf size parameters are associated with decreased % stem loss and maximum stem number. Cultivar was a key driver of the analysis ($F=1.7$; $P=0.002$), indicating consistency in variance of traits between cultivars across multiple years. Correlation between axis one and *A. myosuroides* seed return was significant in years one and three (Figure 3.11). The cultivars Duxford and KWS Santiago occupy opposite domains of axis one, reflecting their respective positioning in terms of suppressive ability (Figure 3.7). This suggests that traits with high loadings within axis one could be considered a 'competitive suite'.

Singularly, the traits with high axes one loadings were also correlated with *A. myosuroides* seed return when examined via Pearson correlation, but not significantly in all three years (Table 3.3). For example, early height could be related to seed return in two of three years. This highlights the value of

multivariate approaches, where cumulative impacts may be observed.

Traits with high loadings along axis one were entered into the linear mixed model based on their loading scores and their scores in the Pearson's correlation. The resulting traits entered were LAR, early height, early leaf width, maximum stem number, early green area, early leaf angle, % stem loss, early leaf length, and SLA.

Table 3.3 - Correlation coefficients of wheat traits in relation to seed production of *A. myosuroides*. * = P<0.05; ** = P<0.01; *** = P<0.001. 2011-12 n=44; 2012-13 n=30; 2013-14 n=30.

Cultivar traits	2011-12	2012-13	2013-14
TGW	-0.0082	-0.0611	**0.5706***
50% emergence	0.0095	0.1455	0.0545
75% spike emergence	n/a	-0.1012	**0.4419***
% stem loss	n/a	0.3236	**0.4906****
Early height	**-0.5362*****	-0.1038	**-0.3793***
Early leaf angle	n/a	0.4072	**0.5220****
Early leaf number	-0.0276	0.2092	0.1905
Early leaf length	n/a	0.1484	-0.1894
Early leaf width	n/a	0.1578	**-0.4129***
Final height	-0.1885	0.0855	0.0306
Final stem count	n/a	-0.2404	-0.3492
Flag leaf SLA	n/a	n/a	0.1683
Flag leaf angle	n/a	0.3958	0.0945
Flag leaf area	n/a	-0.2403	0.1683
Flag leaf length	**-0.3997***	-0.1554	0.1278
Flag leaf width	-0.2077	-0.2183	-0.021
Maximum stem number	**0.3301***	0.096	**0.5573****
LAR	**-0.3555***	**-0.4804***	**-0.5228****

LWR	0.1448	-0.2774	-0.1129
Max. growth rate	0.2135	0.0928	0.3798
NAR	-0.1469	0.0275	0.1919
RGR_W	-0.1589	0.0581	-0.2383
RGR_{GA}	-0.1219	0.0172	-0.1451
SLA	**-0.4518****	-0.141	**-0.3693***
Rate of tillering	0.1005	0.4012	0.2775
Time of max. growth rate	0.0113	-0.0093	0.2892
Time of max. stem number	0.2794	-0.3387	0.2356
Aboveground weight	**-0.3722***	-0.2274	-0.2269
RWR	0.1244	0.1664	0.0615
Early green area	**-0.4417****	-0.3571	**-0.5024****

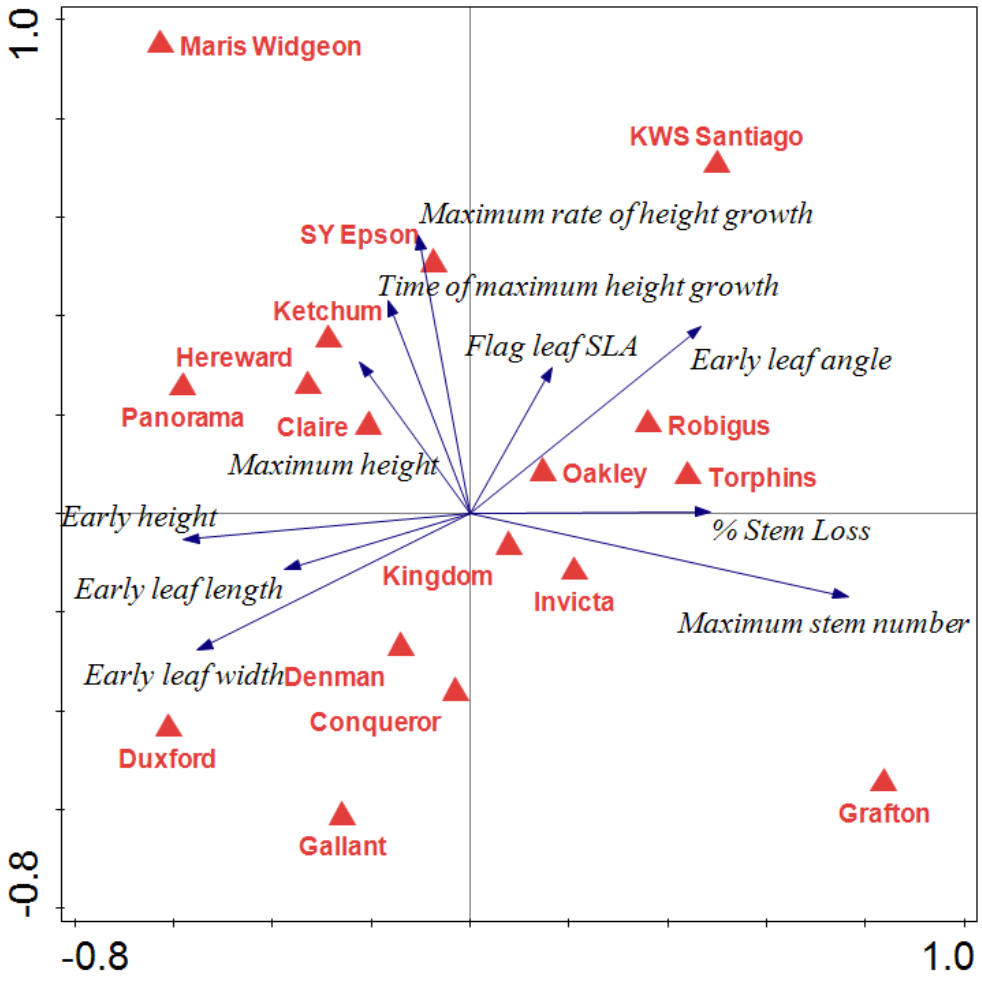

Figure 3.10 - Redundancy analysis ordination plot of wheat traits, with wheat cultivar as the explanatory variable and year as a covariate. Axis one accounts for 19.68%

of the variance, and the cumulative variance in 31.24% (F=1.7, P=0.002). The ten traits with the highest loadings are shown.

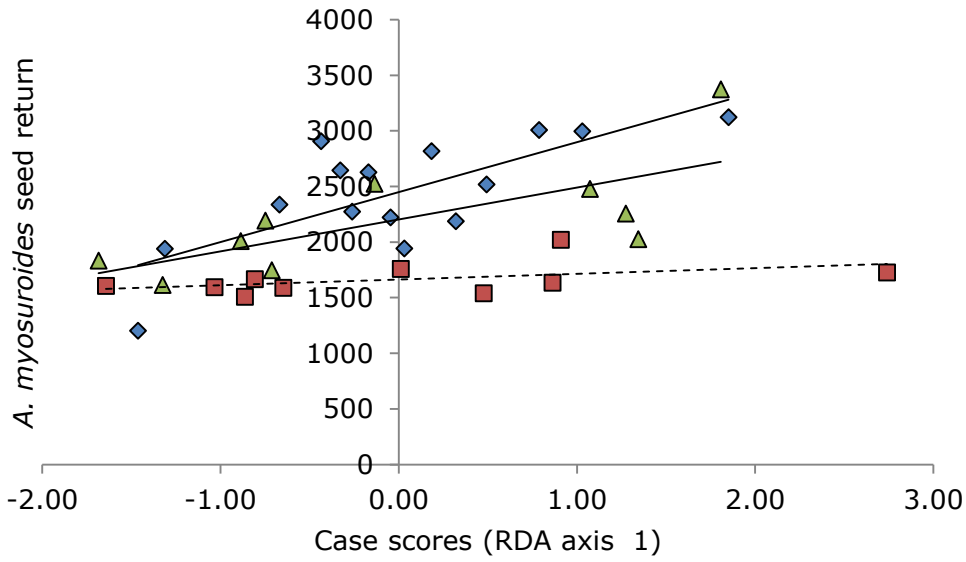

Figure 3.11– Redundancy analysis case scores (axis one) correlated to seed return over the three experimental years. ◆ = 2011-12 (P=0.0015; r^2=0.7441), ■ = 2012-13 (P=0.1954; r^2=0.4468), ▲= 2013-14 (P=0.0205; r^2=0.7137).

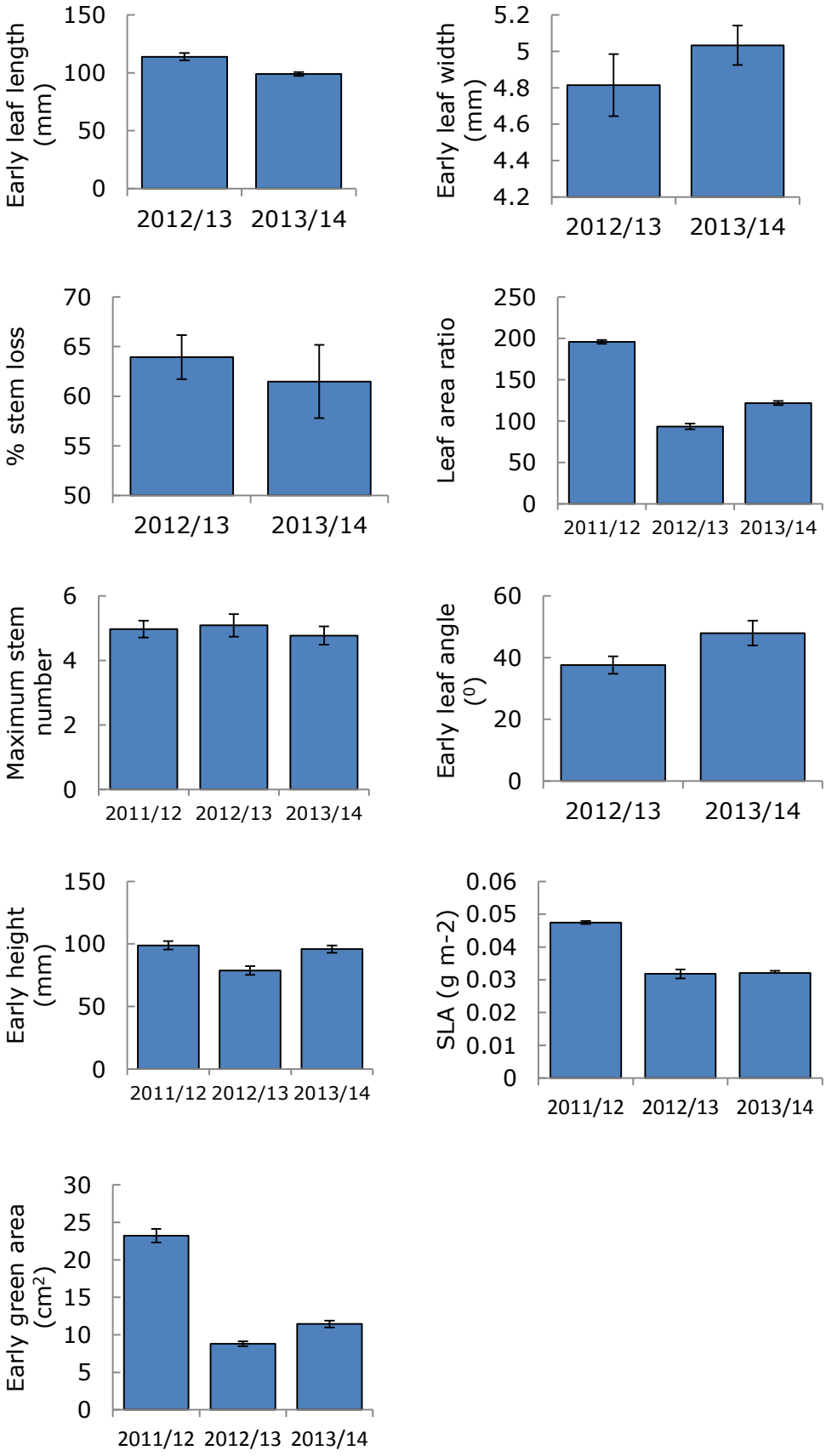

Figure 3.12 – Mean values per year of traits included in the LMM analyses, with s.e. bars.

3.4.2.1 *Linear mixed model*

The linear mixed model suggests that the most reliable estimates of a cultivar's ability to suppress *A. myosuroides* are traits related to early light capture (increased LAR and more erect leaves) and increased stem retention (Table 3.4). Year was also a strong determinant of *A. myosuroides* seed return, but did not interact with the three significant traits.

Table 3.4 - Statistical output of the full linear mixed model. Experimental year 2011-12 was dropped from the model as some traits were not measured in this year. All terms were included in the model, and sequentially dropped in order of least significance from part (b), until remaining values all possessed a significant P-value. Residual variance 0.00524 (s.e. 0.00133).

Fixed term	Wald statistic	n.d.f.	F statistic	d.d.f.	F pr
Sequentially adding terms to fixed model					
LAR	12.62	1	12.62	44.6	<0.001
% stem loss	15.77	1	15.77	21.6	<0.001
Early leaf angle	24.84	1	24.84	46.3	<0.001
Year	20.95	1	20.95	43	<0.001
Dropping individual terms from full fixed model					
LAR	9.03	1	9.03	44.6	0.004
% stem loss	7.77	1	7.77	21.6	0.011
Early leaf angle	4.21	1	4.21	46.3	0.046
Year	20.95	1	20.95	43	<0.001

However, the analysis excluded 53 of 105 of the units as a result of zero weights and missing values. This has resulted in data from 2011-12 being less well represented in the analysis. To allow for inclusion of year one data, traits that were not measured in 2011-12 were removed from the analysis (early leaf width, early leaf length, maximum stem number, % stem loss and early leaf angle). This model continues to report that traits associated with early light capture are important predictors of suppressive ability. Leaf area ratio remains a strong predictor, and early green area and early height also

emerge as predictors. The interaction with year is necessary to consider in early height (Table 3.5).

Table 3.5 - Statistical output of full linear mixed model. Traits not collected in 2011-12 were eliminated to allow the analysis to run for all three years. All terms were included in the model, and sequentially dropped in order of least significance from part (b), until remaining values all possessed a significant P-value. Residual variance 0.000499 (s.e. 0.000654).

Fixed term	Wald statistic	n.d.f.	F statistic	d.d.f.	F pr
Sequentially adding terms to fixed model					
LAR	19.39	1	19.39	91.3	<0.001
Early height	14.11	1	14.11	95.5	<0.001
Early green area	7.85	1	7.85	90.3	0.006
Year	41.86	2	20.4	19.3	<0.001
Year x Early height	6.35	2	3.17	93.3	0.046
Dropping individual terms from full fixed model					
LAR	5.19	1	5.19	91.3	0.025
Early green area	7.71	1	7.71	90.3	0.007
Year x Early height	6.35	2	3.17	93.3	0.046

3.5 **Discussion**

Covariance between plant traits can be a common occurrence. This presents difficulties in interpreting the results of univariate statistical approaches. However, it may also present the opportunity to identify a small number of indicator traits that could be used in a screening protocol that represented a wider suite of suppressive traits. Multivariate approaches make it possible to study this by simplifying various traits into a number of axes.

RDA axis one was related to *A. myosuroides* seed production, meaning that it may be regarded as representing a 'weed suppressive' suite of traits. Although many traits that were components of axis one are related to *A. myosuroides* seed return when examined via univariate approaches, not all were, and only LAR is significantly correlated across all three years.

This emphasises that these traits behave in a cumulative manner. Cultivars represented at the extreme ends were, typically, those that were strongest (Duxford) or poorest (KWS Santiago, Grafton) suppressors of *A. myosuroides*.

However, some cultivar rankings along the axis differed from those determined by *A. myosuroides* seed return. Because the multiple comparisons of cultivars only detected significant differences in cultivar suppressive ability when 2012-13 was removed from the analysis, comparing the rankings along axis to the multiple comparisons rankings must be treated with caution. If the differences are relevant, this could suggest that the traits of high loading are not the only traits associated with suppressive ability. For example, the results of this study have not determined which traits make cultivars like Robigus suppressive. Possible candidates include belowground traits and allelopathic potential (Bertholdsson *et al.*, 2012; Satorre & Snaydon, 1992).

The traits with high loadings in the analysis included early height and parameters relative to early 'leafiness' (such as early leaf width and length) at one axis extreme, with maximum stem number and % stem loss at the other. Seedling leaf area measures have been used as a measure of early vigour in wheat (Rebetzke & Richards, 1999), so the cluster of traits at this end of the axis could be considered 'early vigour' traits. A greater leaf area index conferred greater suppressive strength in spring wheat (Huel & Hucl, 1996), and length and width of leaves one and two negatively correlated with weed fitness (Vandeleur & Gill, 2004; Zerner *et al.*, 2008).

The importance of greater height and upright leaves at early growth stages is contrary to what some would expect, as

prostrate cultivars are considered better able to smother weeds (Huel & Hucl, 1996; Hoad *et al.*, 2006). Why a more erect seedling is more competitive is uncertain, though could be an indication of the growth form of the cultivar at later stages of development. Another suggestion is that early height and upright leaves will increase the amount of far-red radiation reflected by the crop onto *A. myosuroides*. Increased far-red light has been shown to prompt shade-avoidance responses in plants, which will increase upwards growth in anticipation of light competition (Ballare, 1999; Liu *et al.*, 2009). This is typically done at a cost to tiller production. If this behaviour is exhibited by *A. myosuroides*, lower tiller numbers would result, leading to a decrease in seed production.

The traits related to stem production and retention could be classified as 'conserved tillering' traits. In a weedy scenario, a conserved strategy to tiller production would result in resources being allocated elsewhere, enhancing resource acquisition and reducing stem loss in competitive scenarios. The role of stem number in competitive outcomes is difficult to define, as it will vary according to density of the stand. This may explain why there is no consensus on their role in suppressive ability (see section 1.4.4). Additionally, studies tend to focus on final stem number, rather than examine the dynamics of tiller production throughout growth. Tiller production in weedy scenarios merits further study. It may imply that in the UK, allocating resources elsewhere is a safer strategy in weed control.

Though not represented on axis one or indicated in the LMM, a shorter time to spike emergence was related to suppressive ability in the univariate analysis. 'Developmental speed' traits have been related to weed suppression in other studies. Huel and Hucl (1996) reported that early spike emergence confers

increased suppressive ability, but the opposite has also been reported, and suggested to be related to weather conditions (Coleman *et al.*, 2001). Mason *et al.* (2008) used change in spike colour to 'tan brown' as a measure of maturity, finding early maturity was beneficial to weed suppression, but was not apparent across all the weed densities that were tested. The importance of rapid height development in suppression of weeds has been reported (Olesen *et al.*, 2004; Christensen, 1995; Ogg & Seefeldt, 1999). Although this study did not find rate of height development to be important, the result for early height implies explicit examination would assist in understanding its role in UK arable agriculture.

Classifying traits on axis one as being 'early vigour' traits and 'conserved tillering' traits reveals that the 'early vigour' traits were more consistent drivers of separation across the three years. As they appear early in a cultivar's development, these traits would be less prone to the influence of environmental conditions as the 'conserved tillering' traits. The stability of the 'early vigour' traits has been observed elsewhere (Olesen *et al.*, 2004), whilst tiller production and loss have been shown to change according to seasonal conditions (Hoad *et al.*, 2006). The colder and prolonged winter of 2012-13 could explain the limited difference in cultivar suppressive ability, and have strong implications for the importance of the 'conserved tillering' traits in competitive interactions.

Although the traits of the barley and oat cultivars were excluded from analyses for ease of interpretation, their ability to suppress *A. myosuroides* separated them from wheat cultivars. In years 2011-12 and 2013-14, the barley cultivar (Volume) was the strongest suppressor, whilst the oat cultivar (Gerald) was the weakest. Barley and oats are widely considered more

competitive than wheat, and an oat – barley - wheat order of suppressive ability has been supported by the literature (Seavers & Wright, 1999). Why these findings are not reflected in this study is not clear, though could be due to experimental conditions that particularly disfavoured oats (or Gerald, more specifically). In this study, oat was not only a poor suppressor, but its short early stature, delayed maturing and greater tiller number means that it fits the 'poor suppressive' ideotype as determined in these experiments. The inclusion of only one oat cultivar in this study means that generalisations about oats cannot be made. In addition, in the field these species are sown at different times in the autumn period. Whilst comparing them when sown at the same time makes it easier to explore the traits across the species, it does not reflect what occurs *in situ*.

The use of containers presented an opportunity to examine traits in an environment with some controls, whilst being exposed to similar climatic conditions to the field. Nonetheless, it is important to acknowledge the shortcomings of the approach. For example, the containers would have permitted little space for root expansion compared to that seen in the field. This may have important implications for suppressive ability *in situ*, especially in the latter part of the season where belowground resources may become limiting. The degree to which water was limiting would have also differed to the field due to the supplementary watering implemented to prevent excessive drying of the soil. In addition, the container soil was prone to freezing, which would restrict growth more than would be seen in-field. Validation of the experiment in-field (Chapter Four) may reveal if these differences, and others, have an impact on competitive outcomes.

Traits have been used to predict the suppressive ability of barley cultivars (Hansen *et al.*, 2008). In this study, both models suggested the use of traits related to early light capture, in some instances prior to tillering (such as angle of leaves one and two). Early leaf angle can be difficult to measure, LAR would require whole-plant harvesting and estimating % stem loss would be beyond a simple screening process. The value of early height may be undermined by the interaction with year, but its use alongside other traits would strengthen the predictive value of the model across years with highly variable weather conditions. Due to their relevance and comparative ease of measurement, the use of early height and early leaf parameters would be recommended.

3.6 **Conclusion**

In summary, analyses suggest that a group of competitive traits have been identified. These traits include early height, early leaf angle, early green area, LAR and % stem loss. The importance of this suite appeared to decrease in the 2012-13, which may be a reflection of development being arrested due to colder conditions. If a screening protocol was to be developed and predictions made available to growers, it would need to be with the caveat that in colder seasons cultivars are unlikely to differ in their ability to suppress *A. myosuroides*.

This experiment was conducted in outdoor containers, so the importance of these traits needs to be confirmed *in situ*. This experiment and results are described in Chapter Four

4 Chapter four - The traits that govern cultivar suppressive ability and tolerance: results from field experiments

4.1 Introduction

In Chapter Three, a number of related traits were identified that could be used to explain the ability of cultivars to suppress *A. myosuroides*. These experiments were conducted in containers on outdoor sand-beds. This chapter seeks to verify the findings of Chapter Three in a field experiment. Ideally, traits will be identified that are related to suppressive ability and could be used to design a screening protocol to rapidly and non-destructively assess and predict cultivar suppressive ability. Additionally, the field experiment will examine the ability of these cultivars to resist yield loss (tolerance) in the presence of weeds.

4.1.1 Tolerance and associated traits in wheat

Tolerance ability is defined as the ability of a species to resist the suppressive effects of another species (Goldberg, 1990). In arable agriculture, it represents the ability of a crop to maintain yield despite the presence of weed populations. (Cosser *et al.*, 1997; Kirkland & Hunter, 1991). Although on its own it will not contribute to weed seed-bank management, the ability to resist yield loss would have value on sites with problematic weed populations. However, knowledge of a cultivar's ability to tolerate weed pressure is often anecdotal, and so is rarely used as a tool for maximising yield. As weed control becomes increasingly difficult because of the development of herbicide resistance, tolerance of weed competition may become more of a target for breeders in the future.

A number of cereal traits have been related to tolerance, but tolerance has been observed to vary little between cultivars (Jordan, 1993; Olesen *et al.*, 2004), and can be temporally or spatially inconsistent (Cousens & Mokhtari, 1998; Olesen *et al.*, 2004). Additionally, there is no strong consensus on if, or how, tolerance and suppressive ability are related (Watson *et al.*, 2006; Miller & Werner, 1987; Goldberg & Landa, 1991). An understanding of the traits that drive suppressive and tolerance ability will provide insight as to any linkage between them in cereals, which could provide breeders for target traits to incorporate both strategies into new cultivars.

4.1.2 Competitive ability and yield potential

The Green Revolution saw the development of semi-dwarf cultivars with an elevated yield potential, but with a reduction of competitive ability. This has been attributed to changes in resource allocation from the stem to the seed head, with the resulting reduction in height at maturity having a negative impact on both suppressive ability and tolerance (Sinclair, 1998; Challaiah *et al.*, 1986). If traits can be found that improve competitive ability without consequentially reducing yield potential, they would be valuable traits for breeding programmes.

4.2 Aims

In this chapter, the following hypotheses will be tested:

1. Wheat cultivar traits can be associated with cultivar suppressive ability against *A. myosuroides* in the field.
2. Wheat cultivar traits can be associated with cultivar tolerance to *A. myosuroides* in the field.
3. The traits associated with suppressive ability and tolerance are stable across two experimental years.

4. Suppressive ability and tolerance are related, and this can be explained through shared traits.
5. There is a relationship between traits associated with competitive ability (suppression and tolerance) and yield in weed-free scenarios.

4.3 Materials and methods

4.3.1 Cultivar choice

The wheat cultivars investigated in the field were Claire, Conqueror, Duxford, Gallant, Grafton, Hereward, KWS Santiago, Oakley, Panorama and Robigus. Wheat cultivars were selected based on observed differences in traits of interest, with reference to those recorded in the 2011-12 container experiment (Chapter Three). No barley or oat cultivars were included due to the complications this would create in managing the experiment. The cultivars Conqueror, Grafton, KWS Santiago and Oakley were sourced from KWS UK Ltd; Duxford, Gallant and Volume were sourced from Syngenta UK, and Panorama and Claire were sourced from Limagrain UK. The model weed for the suppression studies was *Alopecurus myosuroides* (Huds.). Seed was sourced from Herbiseed UK. All seed was stored in a controlled environment room at 18 °C and 65-70% humidity.

4.3.2 Experimental design

In the 2012-13 and 2013-14 seasons, the ten wheat cultivars were drilled at Rothamsted experimental farm, UK. Cultivars were grown either alongside or in absence of *A. myosuroides*, in a split-split plot experimental design composing of three replicates (with replicates being the highest organisational level, then sowing date followed by cultivar plots and 'weedy'/'weed-free' subplots) (see appendices). Randomisation

was determined using Genstat 14. The original intent was to examine the interaction with sowing date, but poor weather in autumn 2012 resulted in the second date not being planted for that year. A second sowing date was achieved in 2013-14. The interaction with sowing date will be discussed in Chapter Five.

Cultivars were drilled at a density of 350 seeds m^{-2}. 'Weed-free' plots were maintained to enable a comparison of final yield between cultivars when growing under *A. myosuroides* infestation, to gain an understanding of any potential trade-offs in suppression, tolerance and 'weed-free' yield. Sub-plot sizes were 9 x 3m (27 m^2). Each plot was separated by a 1.5 m buffer and a 15 m discard between replicates, and the surrounding field was sown with winter wheat. The two experiments were conducted on neighbouring fields, each chosen for low background populations of *A. myosuroides* to allow for its addition where desired and at a standardised rate.

4.3.3 Addition of *A. myosuroides*

Alopecurus myosuroides was hand-sown prior to drilling on the 'weedy' sub-plots. Rate of sowing *A. myosuroides* was determined by estimating the rate of germination of the seed on petri dishes. Seed were placed in dishes lined with three filter papers and soaked in 5.5 ml of water with 2 g L^{-1} potassium nitrate. These were placed in an environmental control cabinet under a 14/10 hr light/dark regime with temperatures at 17°C and 11°C respectively for 14 days. The seed had a 45% germination rate. Seeds were weighed out in seven batches of 100 on a three decimal place balance. The average weight was 0.25g. This figure was used to weigh out an appropriate quantity of seed for each sub-plot, to acquire a density of approximately 80 plants/m^2. It was expected that approximately 30% of viable seed would germinate in the field

(S.R. Moss pers.com.). To achieve a density of 25-100 plants m^{-2}, it was calculated that 13.5g of *A. myosuroides* seed should be sown per 'weedy' plot.

4.3.4 Data collection

4.3.4.1 *TGW*

Thousand grain weight (TGW) was measured for the seed used in each field experiment. As the same seed was used for the experiments described in chapter two, the method can be found in section 3.3.3.7.

4.3.4.2 *Density counts*

Density counts for the cultivars and *A. myosuroides* were conducted on all 'weedy' subplots (Table 4.1). *Alopecurus myosuroides* were counted in six quadrats (0.25 m^2 in 2012-13, 0.5 m^2 in 2013-14), positioned a metre from the plots edge. Cultivars were counted along two 50 cm lengths of rows for each plot. Cultivar counts were conducted prior to tillering, for ease of distinguishing individual plants, whilst *A. myosuroides* were counted following the spring flush.

In the 2012-13 experiment, the background level of *A. myosuroides* was higher than anticipated and included substantial patches. The difficult drilling conditions in 2012 also meant that pre-emergence herbicides could not be used, making control of the *A. myosuroides* on the weed free plots difficult. This resulted in *A. myosuroides* infestation in all split-plots including the weed-free treatments and at inconsistent densities. Density counts were conducted in 'weed-free' subplots on 10 June 2013 to help account for the impact of variable weed density in data analysis.

Table 4.1 - The dates of collection in both experimental years. *As *A. myosuroides* was present throughout the experiment, density counts were also conducted in the weed-free subplots on 10 June.

	Experimental year	
Data collection	2012-13	2013-14
Sowing date	2 Oct	4 Oct
Wheat density counts	29 Nov	26 Oct
A. myo density counts	21 Feb*	5 March
Sampling for early vigour	5 Feb	21 Jan
Stem counts/crop height	Began 14 Nov	Began 29 Oct
Early height	8 Jan	25 Nov
Leaf counts	9 Jan	21 Jan
Biomass harvest	9-10 July	25 June - 10 July
Grain harvest	20 Aug	19-20 Aug

4.3.4.3 *Early vigour traits*

At approximately growth stage 21-23, 10 wheat individuals were randomly selected and removed from each plot at ground level, ensuring the entirety of aboveground growth was taken. In the 2012-13 experiment, material was collected on 5 February 2013, and on 21 January 2014 in the 2013-14 experiment. The material was placed into bags and stored in 4°C room prior to assessment. Aboveground material was dissected into leaf structures, green stem structures (including leaves that had not opened) and pale stem structures (the sections lacking green pigmentation). The area of leaves and green stems was measured with WinDIAS software (as mentioned in 3.3.3). Leaves and stem material were dried at 80°C overnight before being weighed.

From these data, a number of ecophysiological traits relevant to resource allocation and life history strategy could be calculated (as described in section 2.3.2). These traits were limited to aboveground weight (ABGW), green area, leaf area and specific leaf area (SLA), as other calculations require

measures of belowground biomass which was not sampled in the field.

4.3.4.4 *Stems counts and height measurements*

Beginning on the 14 November 2012 and 29 October 2013, stem counts (for *A. myosuroides* and the crop) and crop height measurements were taken monthly. Ten individuals were selected at least one metre from the edge of each split-plot. Though efforts were made to avoid a biased selection of individuals, choices were made by eye. Plant height was measured from the soil to the highest point (without artificial interference) using a ruler. Efforts were made to ensure that stem counts were conducted correctly, but the clustering of seeds that occurs during drilling means count overestimation is possible, as multiple crop individuals may be mistaken for a single individual.

An indication of early cultivar height were chosen from measurements taken on 8 January 2013 and 25 November 2013. These dates were chosen as they represented two early dates of similar photothermal time for each year (185.5 ptt on 8 January 2013, and 185.8 ptt on 25 November 2013). Final stem counts were taken from 18 July 2012 in 2012-13, and on 30 May 2014 in 2013-2014.

4.3.4.5 *Leaf counts*

The leaves on ten random wheat individuals was counted from each plot on 9 January 2013 for the 2012-13 experiment. In the 2013-14 experiment, leaves per wheat individual were counted from the 10 individuals harvested for early vigour assessments on January 21 (section 4.3.4.3). This change was due to time-constraints when collecting data from the 2013-14 experiment, which was larger than the 2012-13 experiment.

4.3.4.6 *Biomass harvest*

The 'weedy' subplots were subsampled for aboveground material, to estimate biomass of the crop and *A. myosuroides*, and to conduct *A. myosuroides* seed counts and further measurements of crop traits. The sampling was carried out on 9 and 10 July 2013 in the 2012-13 experiment, and between 25 June and 10 July in the 2013-14 experiment. Sampling over a longer duration in the 2013-14 experiment was necessary due to numerous factors. These include the larger size of the experiment through the inclusion of a second drilling date, the need for larger sampling quadrats (see below), and the need to process material within a week of its collection leading to delays in further collection. In 2012-13, all plant material above ground level from three 0.25m^2 quadrats in each plot, placed in bags and stored in a 4°C room until further processing. Due to lower *A. myosuroides* density in the 2013-14 experiment, 0.5m^2 quadrats were used to improve sampling.

Sampling was conducted at this time as *A. myosuroides* begins to shed seed in the middle of July. As sampling in this manner is a labour-intensive process, it was determined that measurements of mature crop traits, such as flag leaf size and ear index, would be calculated for the crop biomass collected at this time.

Lodging was observed during the 2012-13 experiment, likely due, in part, to the high density of *A. myosuroides*. Approximately 25% of the crop was observed to have lodged. Lodging occurred just prior to biomass harvesting, meaning plant material within a sampling area was not degrading. As such, sampling continued as normal, though care was taken to avoid locations where lodging had been so considerable as to compromise sampling efforts.

The plant material was separated into wheat and *A. myosuroides*. Wheat grain heads were collected and ear index was calculated as the percentage of seed head biomass to total weight biomass. Although threshing the heads to quantify the weight of grain would have resulted in a measure of harvest index, time constraints did not allow for this and it was assumed that cultivars did not differ in the percentage of straw and chaff in the ears. In 2012-13 all grain heads were removed and weighed separately from the remaining plant biomass calculate ear index. Due to a greater volume of wheat in the larger quadrats in the 2013-14 experiment, ear index was quantified through subsampling.

All seed heads were removed from *A. myosuroides* and placed in a drying room, and seed numbers were estimated as described in section 3.3.3.5. All material of each plant was dried at 80°C and dry weights taken.

Grain yield was harvested from a central 1m strip in each subplot using a Sampo plot combine on the 19 August in 2013, and the 19 and 20 August in 2014. Due to the high background levels of *A. myosuroides*, it was not possible to acquire a 'weed-free' yield measure for 2012-13.

4.3.4.7 *Flag leaf parameters*

Flag leaf angle was measured on 18 July 2013 and 2 June 2014. The cross-point was positioned where the leaf left the stem, with the 90° point aligned with the emerged ear. Angle was measured in relation to how far it deviated from the upright position (0°).

Ten flag leaves were collected in the biomass harvest (section 4.3.4.6). Length and width was measured manually whilst their

area was quantified using WinDIAS. These leaves were then dried at 80°C and weighed to calculate flag leaf SLA.

4.3.5 Statistical analysis

A factorial ANOVA was used to examine the influence of cultivar and year on *A. myosuroides* seed return and the ability of cultivars to tolerate weed pressure. Seed return on a per m^2 basis was not directly comparable between subplots due to the differences in density within the 2012-13 experiment and between the two study years. This was partly accounted for by calculating seed return per *A. myosuroides* individual (seeds $plant^{-1}$), dividing average seed return by average density for the subplot in question. Seed return per plant was square root transformed to account for non-normality.

Alopercurus myosuroides seed return for Oakley in replicate 2 in 2012-13 was not included in analyses as the value deviated strongly from that observed in other replicates and was considered anomalous, likely due to an error in data collection (48.6 seeds $plant^{-1}$; replicate 1 and 3 recorded 2583.3 and 2071.1 seeds $plant^{-1}$, respectively).

4.3.5.1 *Measures of tolerance*

The initial plans to determine the tolerance of cultivars was to compare 'weedy' and 'weed-free' plots. In 2012-13, this was not possible due to a higher than anticipated background population of *A. myosuroides*, with weed density ranging from 35-198 plants m^{-2}. A hyperbolic yield loss curve was therefore used based on weed counts on all plots recorded in June to get an insight into tolerance of cultivars (Wilson & Wright, 1990). All data points were plotted as yield versus *A. myosuroides* density, with the hyperbolic function curve plotted following the formula:

$$Yield = Y_{weedfree} \times \left(\frac{1-i \times D}{(100 \times (1+i \times D/a))}\right) \quad (4.1)$$

The function was fitted to the whole dataset and the residuals of each data point away from the hyperbola was calculated. The resulting 'mean bias error' (MBE) for each cultivar was used to indicate if the yield was higher or lower than expected at a given density of *A. myosuroides*.

In 2013-14, there was no background population. The ability of the cultivars to tolerate the presence of a weed was, therefore, calculated as percentage reduction of yield per *A. myosuroides* individual per m^2. Though density was less variable across the trial than in the previous year, the calculation incorporated 'per *A. myosuroides* individual' in order to account for differences in density observed throughout the trial site. This assumes a linear relationship between weed density and yield loss which is reasonable given the lower weed densities recorded in the 2013-14 experiment (Storkey *et al.*, 2003).

$$YL = \frac{(100 \text{ x } (1 - (Y_{weedy} / Y_{weedfree})))}{D} \quad (4.2)$$

Where YL is % yield loss, Y_{weedy} is yield in subplots hand-sown with *A. myosuroides* and $Y_{weedfree}$ is yield in subplots where *A. myosuroides* was not added and D is density of *A. myosuroides*. These tolerance values underwent probit transformation so they could be treated as continuous data.

Due to different calculations used for tolerance measures in 2012-13 and 2013-14, they report high tolerance as high and low values, respectively. In order to make results comparable, % yield reduction was changed to % of potential yield by subtracting % yield reduction value from 100.

4.3.5.2 *Cultivar traits*

Height and tiller production was modelled using an unconstrained generalised logistic curve and a split-line model, respectively. This is described in sections 3.3.5.3 and 3.3.5.4. Repeated measures was not a concern in the field experiment, as random plants were measured.

Early cultivar height were chosen from 185.8 ptt (8 January 2013) in 2012-13 and 185.5 ptt (25 November 2013) in 2013-14. Final stem counts were taken on 18 July 2012 in 2012-13, and on 30 May 2014 in 2013-2014. Percentage stem loss was calculated from this value and the maximum stem count derived from the split-line model.

The relationships between traits and competitive measures were initially examined via Pearson's correlation. Principal component analysis was used to identify groups of traits that could account for differences between cultivars. The PCA scores for cultivars were regressed against *A. myosuroides* seed return and measures of tolerance, to identify if the PCA axes could be used to represent a 'competitive' suite of traits.

After initial examination using an LMM revealed no evidence of an effect of blocking, multiple linear regression (MLR) was used to identify the traits that provided a good description of *A. myosuroides* seed return. Years were included in analysis, with replicates defined separately from each year due to the two experiments being conducted on different field sites. Traits within years were standardized to zero to account for the influence of year. Traits identified as being related to *A. myosuroides* seed return by the LMM were evaluated using MLR, producing all subsets pairwise and additive models to identify

the optimum number of independent traits that predicted the suppressive ability of wheat against *A. myosuroides*.

Due to the inability to have equivalent measures of tolerance ability across both study years, all-subsets regression was performed for each year independently to determine which traits related to cultivar tolerance. Traits for inclusion were determined by favouring those that were related to tolerance in Pearson's correlation.

4.4 **Results**

Mean daily temperatures through the duration of the experiments were 8.5°C in 2012-13 and 10.5°C in 2013-14 (presented in section 3.4, figure 3.5). Radiation data can be found in figure 3.6. Rainfall is presented in Figure 4.1. Density of *A. myosuroides* and the crop stand varied between the two years. Cultivar density was 114.4 ± 3.45 m^2 in 2012-13, and 281.1 ± 9.07 m^2 in 2013-14. *Alopecurus myosuroides* in 'weedy' subplots was present in densities of 95 ± 5.99 in 2012-13 and 23.3 ± 0.76 in 2013-14. In the subplots intended to be 'weed-free' in 2012-13, there was an *A. myosuroides* density of 69.3 ± 0.81.

The yields from the experiments are presented in Table 4.2. The yields must be considered with care, as it was not possible to maintain weed-free conditions in the 2012-13 experiment, and *A. myosuroides* density was lower in the weedy plots in the 2013-14 experiment.

	weedy' yields				weed-free' yields			
Cultivar	2012-13	s.e.	2013-14	s.e.	2012-13	s.e.	2013-14	s.e.
Claire	1.9	0.578	5.0	0.488	3.0	1.277	12.6	0.518
Conqueror	2.1	0.835	6.8	0.259	3.4	1.196	13.7	0.331
Duxford	3.0	0.699	6.3	0.549	3.9	0.621	13.0	0.339
Gallant	1.6	0.617	5.2	0.109	2.8	1.104	12.5	0.121
Gerald	2.6	0.466	4.8	0.502	3.7	0.552	13.2	0.090
Hereward	1.7	0.563	4.8	0.474	3.4	1.148	10.5	0.187
KWS Santiago	3.0	0.929	7.0	0.555	4.6	0.860	14.0	0.282
Oakley	2.7	0.644	5.2	0.856	3.3	0.667	12.2	0.691
Panorama	2.9	0.272	5.7	0.453	4.7	0.413	12.5	0.251
Robigus	3.5	0.278	5.2	0.442	5.8	0.338	11.7	0.390

Table 4.2. – Yield of cultivars grown in 'weedy' conditions (*A. myosuroides*) and 'weed-free' conditions over two years. Densities of *A. myosuroides* varied within between years, and control of *A. myosuroides* was not achieved in 'weed-free' subplots in 2013-14.

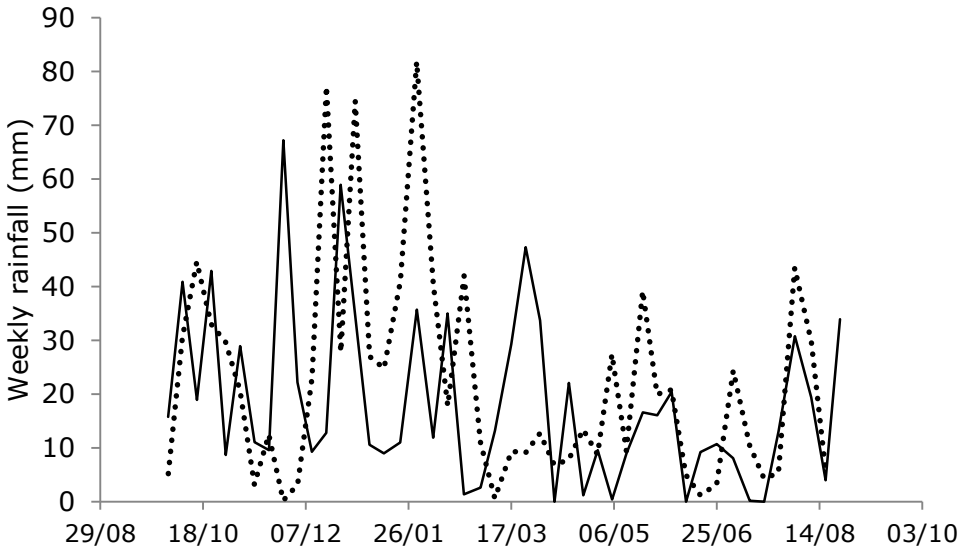

Figure 4.1 - Weekly rainfall at Rothamsted Research, Herts, UK during the experiment. Solid = 2012-13; Dashes = 2013-14

4.4.1 Cultivar suppressive ability and tolerance

Seed return and biomass of *A. myosuroides* were found to be closely related (Figure 4.2). As such, continuing analysis focused on seed return which, in the context of integrated weed management is the focus of this study.

The ANOVA reported no effect of cultivar (d.f. 9; P=0.997) and cultivar by year interaction (d.f. 9; P=0.918). Year was significant (d.f. 1; P<0.001), likely due to differences in *A. myosuroides* density. The impact of year was significant when suppression was calculated as seed return per *A. myosuroides* individual (Figure 4.3), but not when measured on the basis of seed return per m^2 (Figure 4.4). The reduction of per plant seed return in 2012-13 is likely a result of increased intraspecific competition and lower average temperature. There was no evidence that cultivars maintained equivalent suppressive abilities across the two years (r=-0.476; P=0.1643) (Figure 4.5).

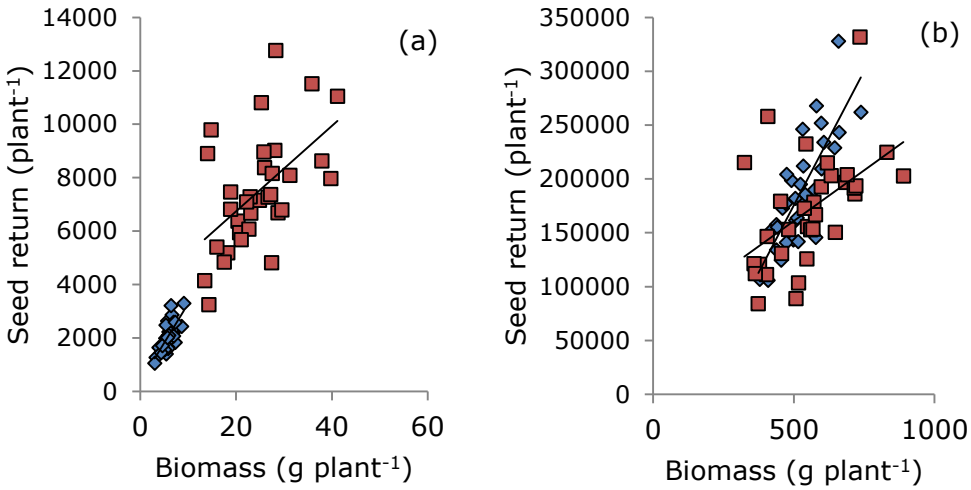

Figure 4.2 - Relationships between *A. myosuroides* seed return and biomass (a) on a 'per plant' (all years R=0.8899; P<0.001) and (b) a m^{-2} basis (all years R=0.5647; P<0.001). Red = 2012-13, Blue = 2013-14

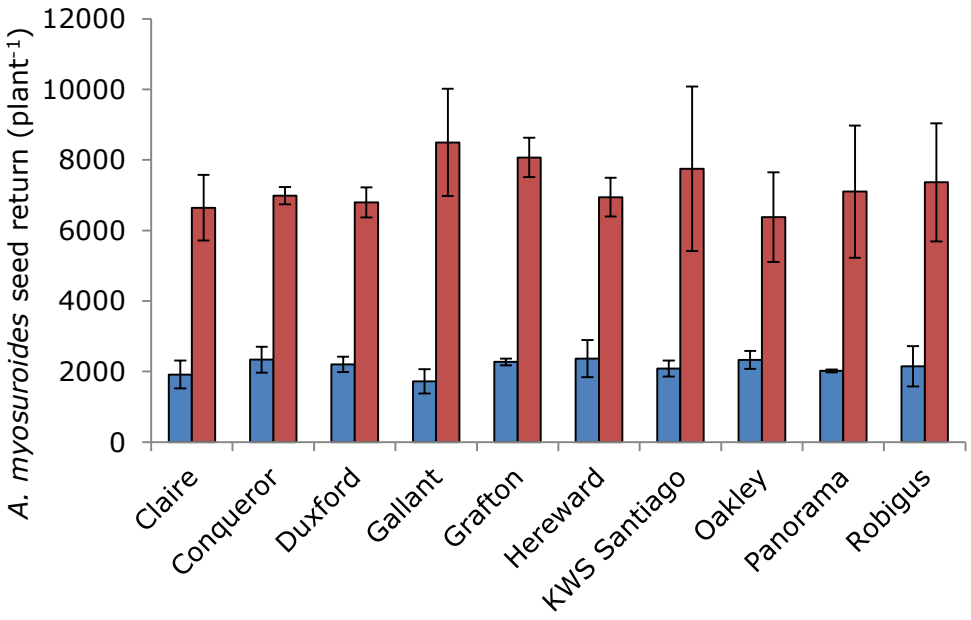

Figure 4.3 - Mean *A. myosuroides* seed return (on a 'per *A. myosuroides* individual' basis) when grown in the field with wheat cultivars in different years. Bars indicate standard error. Blue = 2013-14; Red = 2013-14.

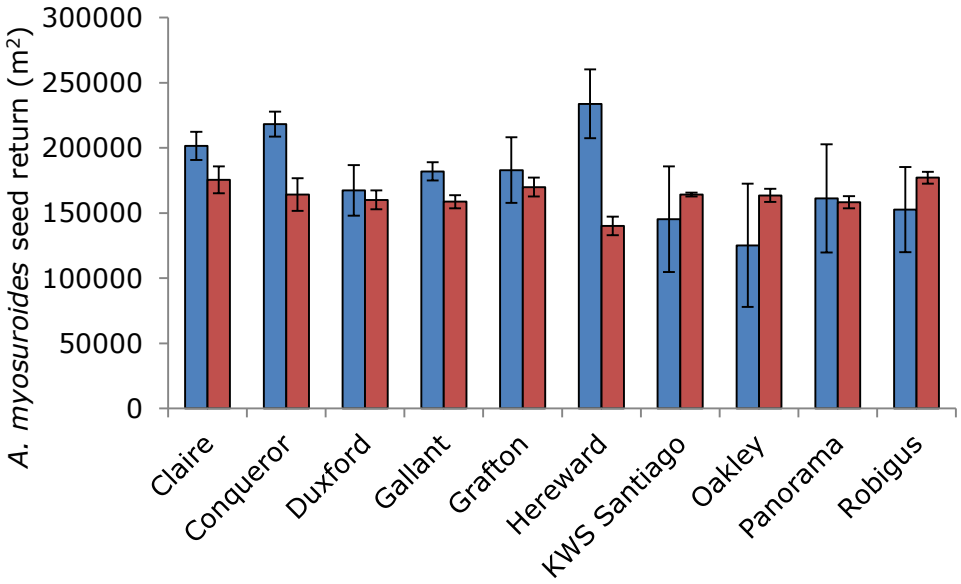

Figure 4.4 - Mean *A. myosuroides* seed return (on a m^{-2} basis) when grown in the field with wheat cultivars in different years. Bars indicate standard error. ANOVA detected no differences between cultivars (d.f. 9; P=0.891), year (d.f. 1; P=0.345), nor a cultivar by year interactions (d.f. 9; P=0.686)

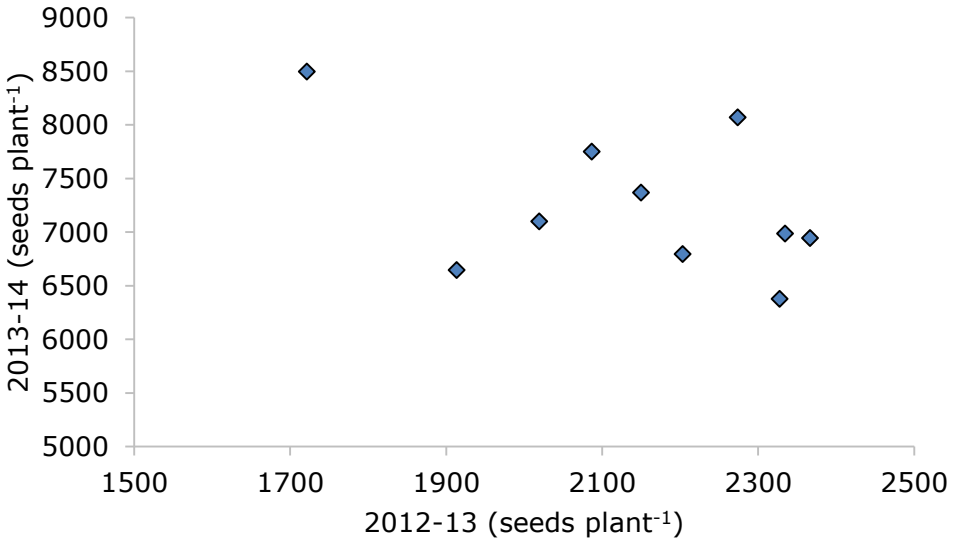

Figure 4.5 - The suppressive ability of cultivars across the two experiments, expressed as seed production of *A. myosuroides* individuals.

Tolerance to *A. myosuroides* pressures was quantified using different measures in each year. Tolerance residuals in 2012-13 represent the difference in anticipated yield under a given weed density and the actual yield (Figure 4.6), whilst 2013-14 represent the % of yield maintained by the stand under *A.*

myosuroides pressure when compared to the weed-free stands. This presents difficulties in assessing a year x cultivar interaction. There were no differences in the ability of cultivars to maintain yield under *A. myosuroides* pressure in either year, but correlation implies that there is some stability in cultivar tolerance over the two years (r=0.669; P=0.024) (Figure 4.9).

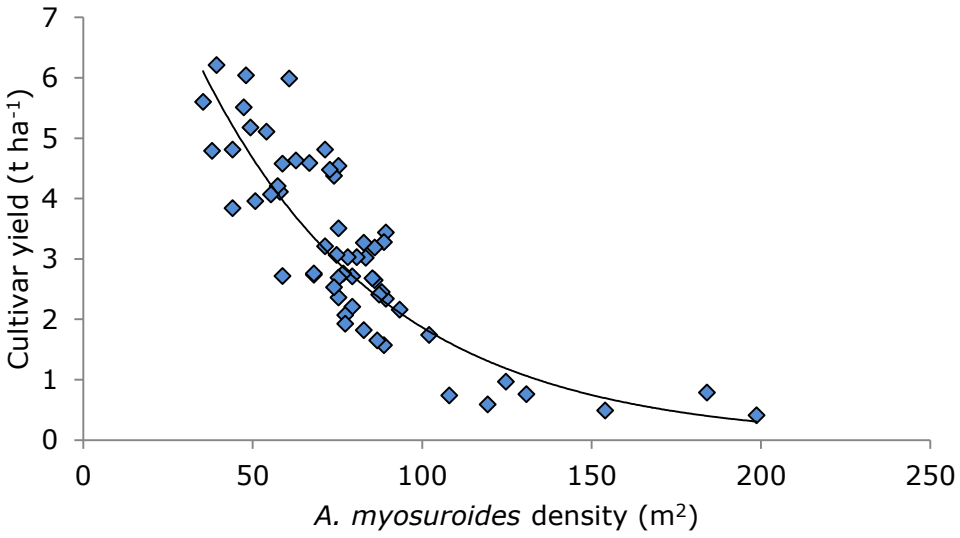

Figure 4.6 - The rectangular hyperbole fitted to cultivar yield under different *A. myosuroides* densities. Residuals were derived for each subplot as a measure of tolerance (see section 4.3.5.1).

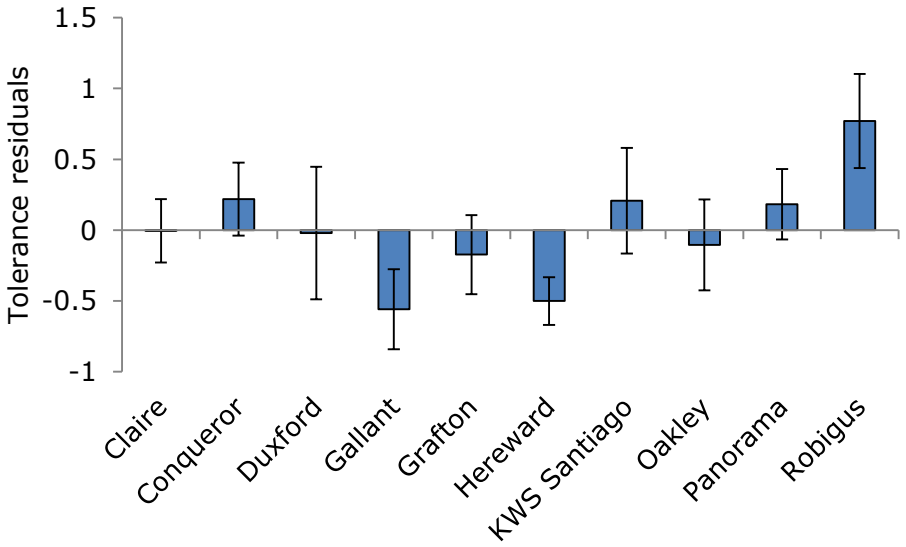

Figure 4.7 - Cultivar tolerance in the 2012-13 experiment, with error bars. (d.f. 9; P=0.175). Cultivar tolerance is represented as the mean bias error of subplot residuals from a rectangular hyperbole of subplot yield and *A. myosuroides* density (see section 4.3.5.1).

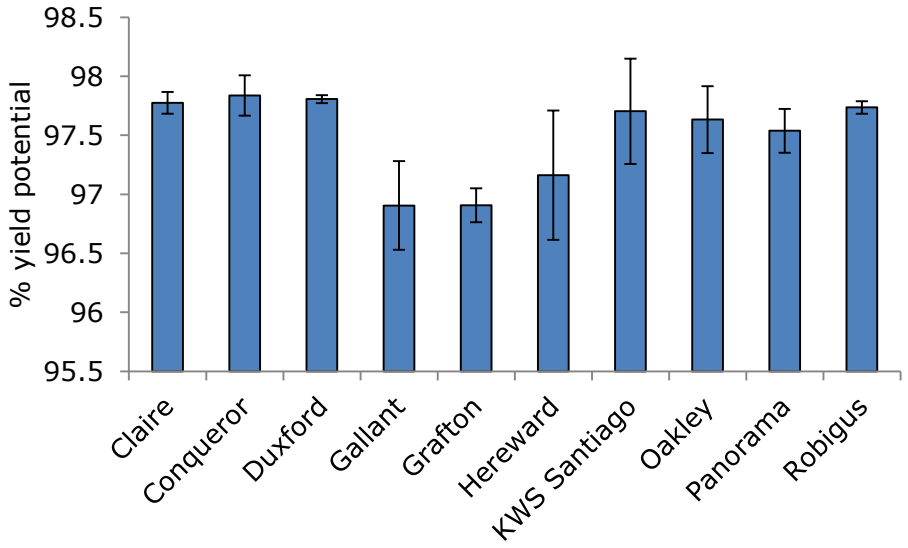

Figure 4.8 - Cultivar tolerance in the 2013-14 experiment, recorded as % of total potential yield under weed pressure, with error bars. (d.f. 9; P=0.678)

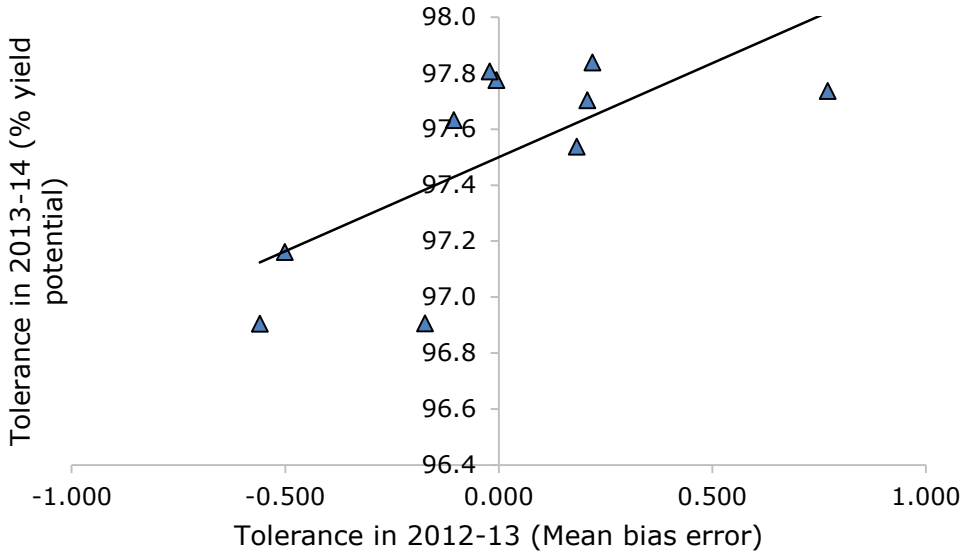

Figure 4.9 - The tolerance of cultivars to *A. myosuroides* in two different years.

4.4.2 Cultivar traits

Pearson's correlation revealed that in 2013-14, traits linked to increased early leafiness and ABGW were related to increased *A. myosuroides* seed return, but not in 2012-13 (Table 4.3), possibly due to colder temperatures impeding growth. These

traits have high co-linearity (Figure 4.12). They dominated PC1 along with % stem loss, TGW and time of maximum slope in 2012-13 (Figure 4.10 and 4.11). Early leaf counts had lower loadings in PC1 in 2013-14, and early height and SLA have higher loadings. Additionally, early green area was negatively loaded in 2012-13 and positively in 2013-14. Linear regression analysis identified no significant relationship between PCs 1 or 2 and *A. myosuroides* seed return or measures of tolerance in both years studied, implying that highly loaded traits do not constitute a suite of competitive traits.

Table 4.3 - Correlation coefficients of wheat traits in relation to seed production of *A. myosuroides* and tolerance. Tolerance measure was residuals in 2012-13 and % of total potential yield under weed pressure in 2013-14 (section 4.3.5.1). * = P<0.05; ** = P<0.01; *** = P<0.001. N=30.

	Seed return		Tolerance	
Cultivar traits	2012-13	2013-14	2012-13	2013-14
TGW	-0.0781	-0.0949	0.0088	0.0585
ABGW	-0.1957	**0.5466****	**-0.459***	-0.2045
Early height	-0.2876	0.2143	0.0377	-0.345
Final stem count	-0.1037	0.2959	**0.5142***	**-0.3995***
Flag leaf SLA	0.0162	0.027	-0.3477	0.1886
Flag leaf angle	0.1492	-0.0399	0.0288	0.2163
Flag leaf length	-0.2369	0.063	0.4396	-0.1538
Flag leaf width	0.1408	0.0543	0.2305	0.1084
Final height	0.3083	0.1559	0.0734	0.1305
Maximum stem number	0.1359	0.2181	0.1403	-0.0223
Early leaf area	-0.1645	**0.4501***	**0.4164***	-0.1216
Early leaf number	0.2197	**0.4968****	0.1548	-0.1851
Time of max. stem number	0.0289	-0.1859	0.0648	0.2157
Rate of tillering	0.1172	0.321	0.027	-0.2565
Early SLA	0.1172	0.0945	0.1586	0.122
Early green area	-0.1496	**0.4708****	**0.4393***	-0.1482
% stem loss	0.2414	-0.0635	**-0.4483***	0.2851
Flag leaf area	0.396	-0.0635	-0.0939	-0.2577
Ear index	0.1689	0.0543	-0.1779	-0.3817
Time of max. growth rate	0.0851	0.0426	0.1964	-0.1258

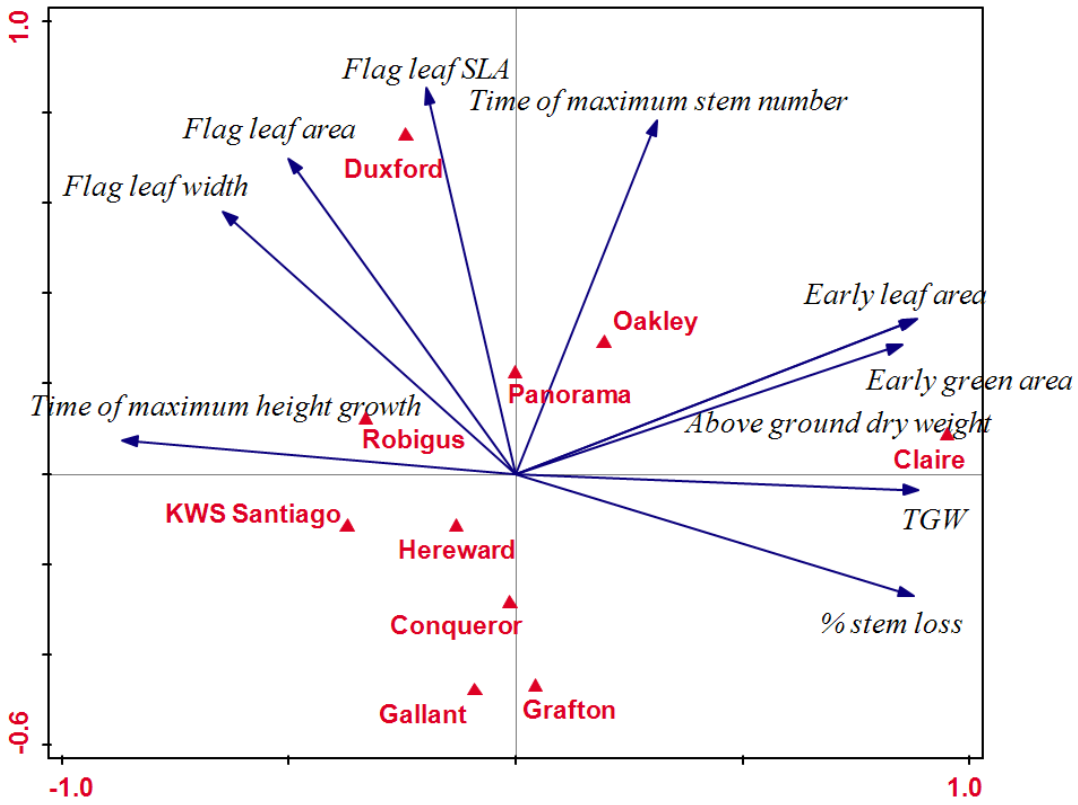

Figure 4.10 - Redundancy analysis ordination plot of wheat traits for the 2012-13 experiment, with wheat cultivar as the explanatory variable. Axis one accounts for 34.83% of the variance, and the cumulative variance in 62.44% . The ten traits with the highest loadings are shown.

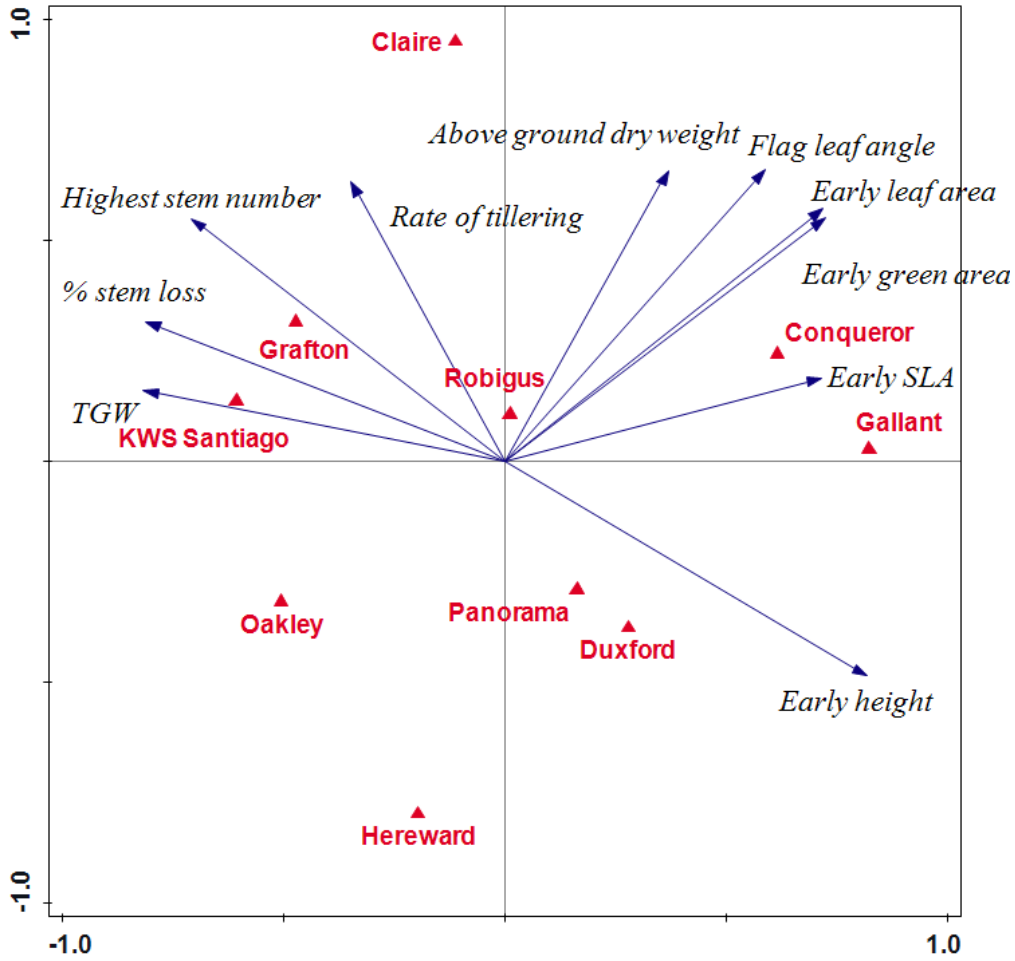

Figure 4.11 - Redundancy analysis ordination plot of wheat traits for the 2013-14 experiment, with wheat cultivar as the explanatory variable. Axis one accounts for 27.15% of the variance, and the cumulative variance in 46.89%. The 10 traits with the highest loadings are shown.

The REML analysis reported that early leaf number, early leaf area, early green area and ABGW are all predictors of *A. myosuroides* seed production. Regression analysis was performed, concentrating on these traits, and concluded that it would be reasonable to suggest that early leaf number alone is a sufficient predictor of suppressive ability (variance accounted for = 86.2% in intra-block regression; 87.3% in REML), with little or no improvements from adding any other variables. There was high co-linearity between early leaf area, early green area and early ABGW (Figure 4.12), indicating that if additional

traits were to be included in a model, only one of these would be required. Parallel line models were best descriptors of early green area, early leaf area, early ABGW and early leaf number, with each line representing a year. Though the parallel lines suggest the same trend but with each year occupying a distinct range, but this relationship is weaker in 2012-13 (Figure 4.13). All other traits fit a parallel flat lines model, with experimental year being the key determinant of differences in seed return.

Regression analyses suggested that in 2012-13, % stem loss was the only trait appropriate for predicting the ability of a cultivar to tolerate *A. myosuroides* pressure, and only in forward and stepwise analysis. All subsets analysis also implied that no strong improvement was acquired from adding other traits. However, it only accounted for 13.29% of variance (increasing to 15.9% if early ABGW weight was included in the model). In the 2013-14 analysis, no traits were important determinants of tolerance ability.

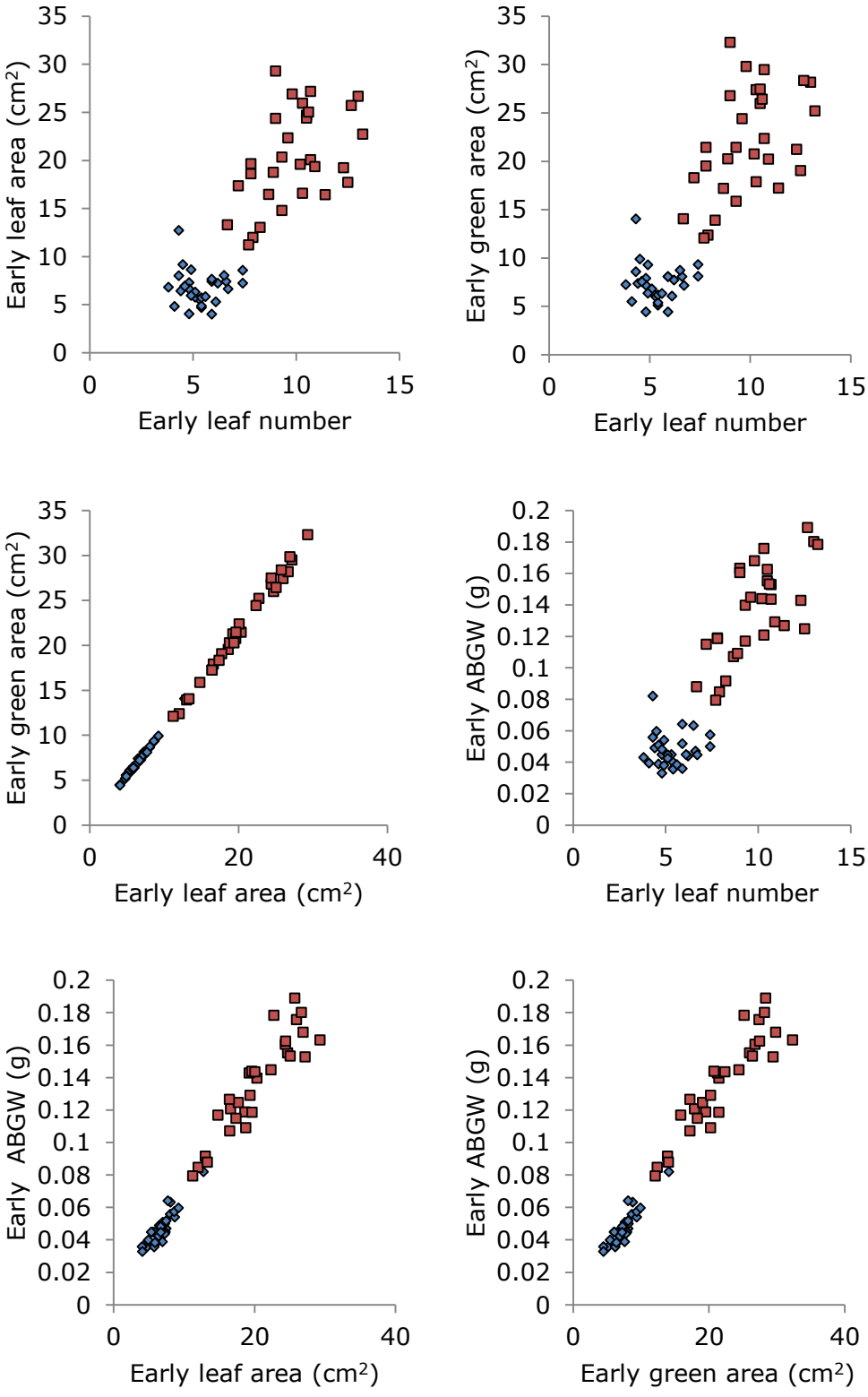

Figure 4.12 - The degree of co-linearity observed across the four traits that were related to *A. myosuroides* seed return in LMM and MLR analyses. ◆ = 2012-13 ■ = 2013-14

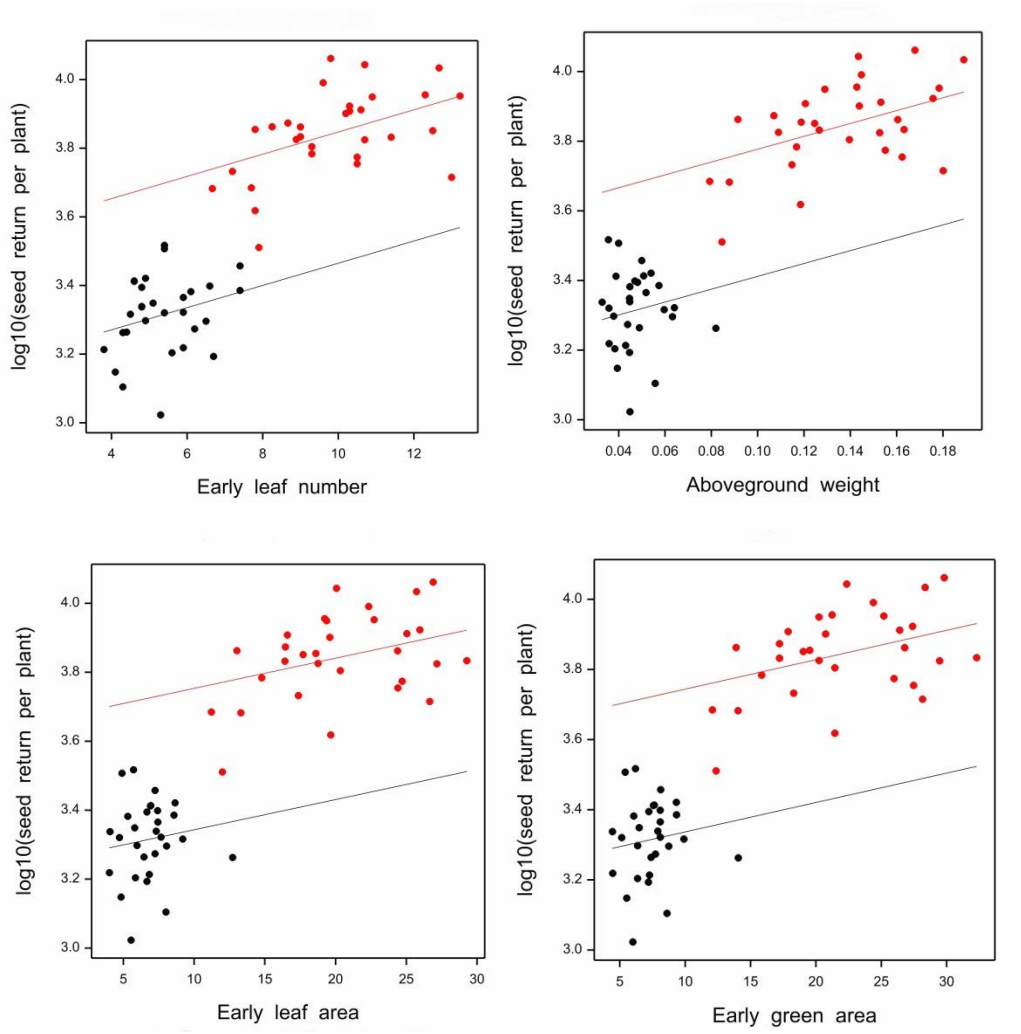

Figure 4.13 - Parallel lines models fitted to the four traits significantly related to *A. myosuroides* seed return. ● = 2012-13; ● = 2013-14.

4.4.3 The relationship between suppressive ability and tolerance

In both study years, a relationship between the measures of tolerance and suppressive ability was observed (though weakly in 2012-13) (Figures 4.14 and 4.15). These results imply that in wheat cultivars, good suppressive ability will coincide with ability to resist yield loss caused by *A. myosuroides* pressure.

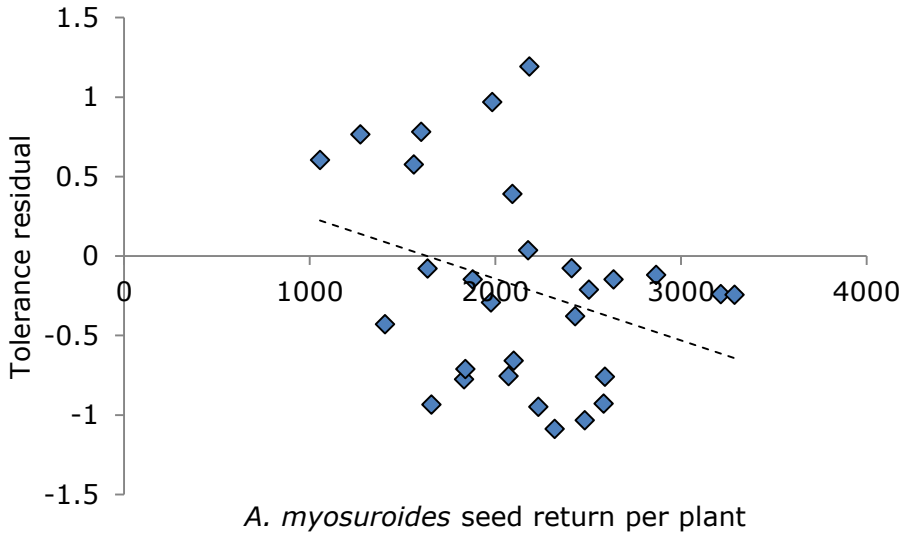

Figure 4.14 – The relationship between tolerance and suppressive ability in 2012-13 (N=30; P=0.0879, r = -0.3225)

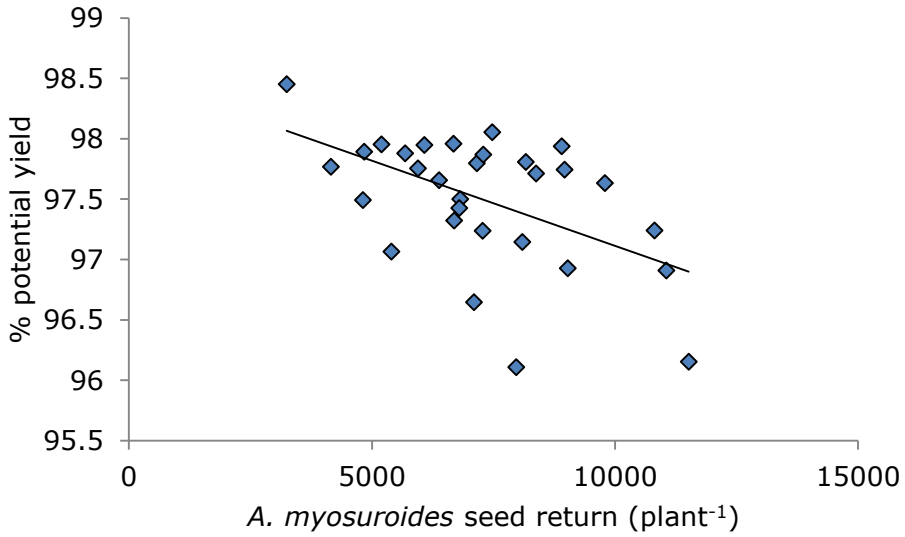

Figure 4.15 - The relationship between tolerance and suppressive ability in 2013-14 (N=29; P=0.0032, r = -0.5199)

4.4.4 Weed-free yield and competitive ability

Due to *A. myosuroides* infestation of all plots in the 2012-13 experiment, weed-free yield could only be investigated in 2013-14. There was no evidence that weed-free yield interacted with measures of suppressive ability or weed tolerance (Figure 4.16). Correlation analysis suggests that the only trait related to weed-free yield was flag leaf SLA (Figure 4.17), which lacks

a correlation with measures of suppressive ability or tolerance (Table 4.3).

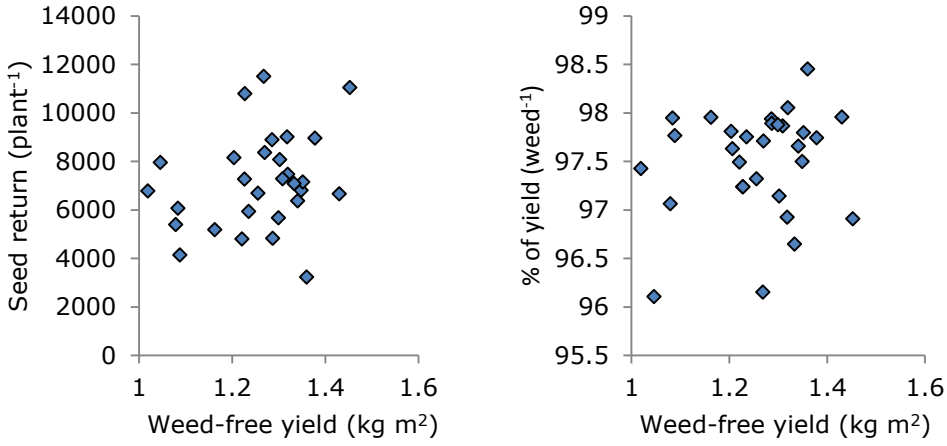

Figure 4.16 – The relationship between weed-free yield and (a) *A. myosuroides* seed return (r=0.2328; P=0.2243) and (b) % yield maintained under weed pressure (per *A. myosuroides* individual) (r=-0.1694; P=0.3796)

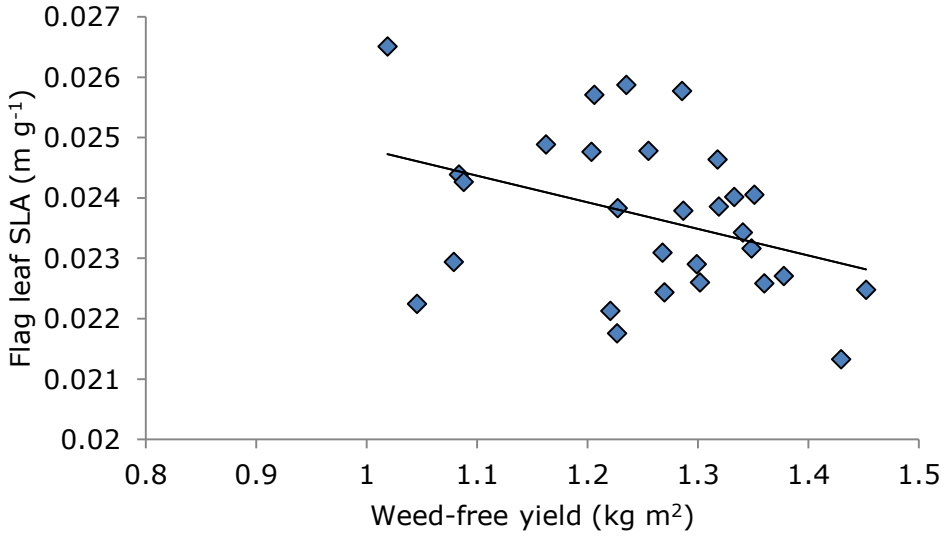

Figure 4.17 - The relationship between weed-free yield and flag leaf SLA (r=-0.3702; P=0.0481).

4.5 **Discussion**

4.5.1 Cultivar performance

No cultivar showed an elevated suppressive ability in either year, casting doubt on the use of cultivars as a means of weed

suppression and seed-bank management. This is counter to findings of other publications looking at suppressive ability (Wicks *et al.*, 1986; Blackshaw, 1994; Christensen, 1995; Huel & Hucl, 1996; Cousens & Mokhtari, 1998; Ogg & Seefeldt, 1999; Worthington *et al.*, 2013). However, inconsistencies between years have been reported in the literature (Seavers & Wright, 1999; Vandeleur & Gill, 2004).

Whilst the literature often supports the notion of sustained differences in cultivars' suppressive ability, this is not always true for tolerance. Though studies have reported difference in the ability of wheat cultivars to tolerate weeds (Appleby *et al.*, 1976; Challaiah *et al.*, 1986; Mennan & Zandstra, 2005), others have not (Cousens & Mokhtari, 1998; Kirkland, 1991). Olesen *et al.* (2004) reported differences in Danish cultivars' ability to suppress weeds, but noted no differences in their ability to tolerate weeds.

However, it is important to consider the impact of different densities of *A. myosuroides* over the two years. An increase in weed density would lead to increased dominance of the stand. This may influence perceived suppressive ability and tolerance (and traits that may be related to each), as the level of competition is different. In lower *A. myosuroides* densities, the wheat would have an initial advantage, which would be amplified as the crop develops. In higher *A. myosuroides* densities, the smothering of the crop may reduce its ability to exert suppressive influences through competition for light.

The lack of significant differences between wheat cultivars in suppressive or tolerance ability in this study may be explained by an observation made by Reeves and Brooke (1977). In a preliminary study of tolerance to yield loss in four cultivars, no

difference was found. But in an expanded study the following year, in which 29 cultivars of both semi-dwarf and 'traditional' cultivars were examined, they observed variation in tolerance. In a study of three cultivars, Cosser *et al.* (1997) reported that Maris Widgeon (a taller cultivar developed in the 1960s) was more tolerant than the two semi-dwarfs in the study. It is possible that this study, which focused on commercial UK semi-dwarfs, represented too few cultivars of similar origin. The drive for higher yielding cultivars under optimum conditions has narrowed the genetic background of wheat, resulting in reduced trait variability and thus reduced variation in tolerance and suppressive ability. There is much research now focussed on increasing the genetic diversity of wheat, which may see the increased variability in competitive traits.

4.5.2 Traits related to competitive ability

Traits related to early cultivar green area (early green area, early leaf area and leaf number) and early ABGW are suggested to be predictors of suppressive ability. Early leaf number (approximately growth stage 21) would be the recommended indicator. However, an increase in traits related to green area and early ABGW resulted in the reduced suppressive ability of a cultivar. The converse would be expected as greater occupation of space would augment the ability of the crop to compete for light and smother weeds (Fang *et al.*, 2011; Hoad *et al.*, 2006; Lemerle *et al.*, 1996). Increased early leaf width, a component of early leaf area, has been linked to increased early vigour (Rebetzke & Richards, 1999), and has been related to suppressive ability (Huel & Hucl, 1996; Kropff & Spitters, 1992). Rapid leaf area development, specifically, has been linked to increased suppressive ability (Coleman *et al.*, 2001). The implication in this study would be that lower vigour is

associated with increased suppressive ability. However, this study considered all leaves present at approximate GS 21-23, so may not represent good indicators of early vigour.

One possible explanation is that this result does not account for arrangements and angle of leaves, which could alter the ability of the crop to intercept light (Hoad *et al.*, 2006). Another is that competition for belowground resources are more important in the field. Cultivars seedlings with a high investment in aboveground structures may have less invested in roots, as was seen in Chapter Two. As such, the observed relationship may be due to the investment in roots, which results in competitive strength. This importance of drought in competitive scenarios has been highlighted in a simulation model analysing the potential impact of climate change on crop - weed interactions (Stratonovitch *et al.*, 2012).

From these results, it is difficult to determine if any trait could be consistently related to the ability of wheat cultivars to tolerate the presence of *A. myosuroides*. Stem loss in 2012-13 may have been of elevated importance due to relatively high weed densities, equating lower stem counts and, correspondingly, decreased yield (Appleby *et al.*, 1976; Hucl, 1998). As such, a lower stem loss score may reflect tolerance through the ability of cultivars to maintain tillers under weed pressure. However, stem loss was higher in 2013-14, whilst final stem counts and maximum stem numbers were lower (see appendices). The complex interplay between these three traits, and difficulty in their quantification, means that stem loss is unlikely to be a reliable candidate for predicting tolerance to *A. myosuroides*. Evidence of other traits involvement in cultivar tolerance was lacking. Greater height and larger leaves at maturity have been linked to increased tolerance of weeds

(Appleby *et al.*, 1976; Challaiah *et al.*, 1986; Coleman *et al.*, 2001; Vandeleur & Gill, 2004), but not in this study.

The literature has examples of cultivar tolerance traits varying over both locations and years (Cousens & Mokhtari, 1998; Didon & Hansson, 2002; Zerner *et al.*, 2008). Important tolerance traits changing over years could support the idea that tolerance to weed pressure is not a trait in itself. Wang *et al.* (2010) suggested that tolerance ability is a collection of stress-resistant traits. As such, the importance of different traits may instead reflect different stresses imposed by a weed species and environmental conditions in each year. For example, weed species *B. tectorum* is strongly competitive for water, and so tolerance could partially depend on a cultivar's ability to tolerate drought stress and compete for water (Blackshaw, 1994). Under this assumption, differences in climatic conditions or other unquantified factors may have contributed to the change in tolerance predictors between the two years.

4.5.3 Tolerance versus suppressive ability

The value of tolerance and suppressive ability are quantifiably different, justifying their examination as separate traits. Whilst the suppression of a weed species would reduce its seed production, tolerance maintains yield but may permit the weed's presence in the seed-bank to increase. This has been observed in tolerance studies (Appleby *et al.*, 1976). A cultivar that is able to combine both high suppression and tolerance against *A. myosuroides* would be of greatest value to UK arable farmers.

The relationship found between suppression and tolerance is a promising result, implying that these modes of competition co-occur. This is in agreement with other studies looking at wheat

cultivars (Huel & Hucl, 1996; Challaiah *et al.*, 1986; Lemerle *et al.*, 1996). The observed relationship may, in part, be a result of the reduced ability of an *A. myosuroides* population to make a competitive impact on a wheat cultivar if the cultivar has been able to suppress the growth of the weed. Early ABGW is implied to be a shared trait, and lower ABGW could serve as a useful indicator of both reduction of *A. myosuroides* seed return and increased ability to tolerate weed pressure. However, it is unlikely to be a reliable measure if used on its own. Caution will also be required, given that the relationship between ABGW and suppressive ability is counter to that which has been seen in other studies (Bertholdsson, 2005; Bertholdsson, 2011).

Though principal components one or two were not related to suppression or tolerance, PC1 was highly loaded for traits related to early green area (suppressive ability trait) and % stem loss (a tolerance trait in 2012-13). In 2012-13, the PCA reported early green area and % stem loss to be positively associated with one another, but this relationship reversed in 2013-14. Another trait dominating PC1 was TGW, which maintained a positive association with % stem loss, whilst early green area switched from positively to negatively associated from 2012-13 to 2013-14. This implies that early green area is the trait behaving in an unexplained manner, suggesting that there is a complex level of interplay between these traits in UK commercial wheat cultivars. The positive relationship between seedling leaf area and seed weight has been noted in bread wheat, and their combined contribution to early vigour ascertained (Maydup *et al.*, 2012). Murphy *et al.* (2008) also noted a positive relationship between leaf area index and TGW. Why the association between TGW and early green area should reverse between the two years is uncertain.

4.5.4 Yield penalties

The lack of significant relationship between weed-free yield and both suppressive ability and tolerance, and lack of shared traits, suggests that these two modes of competition could be enhanced through breeding without a penalty to yield. This is in agreement with other studies (Vandeleur & Gill, 2004; Coleman *et al.*, 2001; Huel & Hucl, 1996). However, a trade-off between competitive ability and yield potential is known to exist, largely manifest through increased mature height (Challaiah *et al.*, 1986; Siddique *et al.*, 1989). That mature height is not related to suppression, tolerance or weed-free yield in this study does not challenge the existence of this trade-off, but may be due to the similarity in height between the semi-dwarf cultivars included in this study. As such, if the cultivars in the study had been more varied (not just drawn from UK commercial semi-dwarfs), relationships not observed here may have been reported. This may apply to all traits explored in this study.

4.6 Conclusions

In summary, no differences in cultivar ability to suppress or tolerate *A. myosuroides* were found in the field. Although traits were associated with both suppressive ability and tolerance, they frequently varied over years or explained little variance. This supports the requirement for a means of assessing competitive ability using numerous traits to enhance the accuracy of predictions (Lemerle *et al.*, 1996). The similarity of the cultivars in this study may have obscured the contribution of other traits that have been associated with competitive ability in the past. Such traits include mature height (Vandeleur & Gill, 2004; Lemerle *et al.*, 1996; Appleby *et al.*, 1976; Challaiah *et al.*, 1986; Ogg & Seefeldt, 1999), rate of height development (Olesen *et al.*, 2004; Christensen, 1995; Ogg & Seefeldt, 1999),

and various tillering traits (Lemerle *et al.*, 1996; Korres & Froud-Williams, 2002).

Conclusions of this experiment must be drawn with caution. Comparisons between years and examination of year interactions, will have been compromised due to different cultivar and *A. myosuroides* densities. Higher density of *A. myosuroides* in 2012-13 likely results in increased interspecific competition and smothering of the crop, and lodging was frequently observed. Some of the variation in crop traits between the two years may be attributed to phenotypic component of traits, though the extent to which could not be ascertained.

5 Chapter five – Suppressive crop traits and their interaction with sowing density, drilling date, and weed species.

5.1 Introduction

In the previous chapters, the potential relationship between various cultivar traits and suppression of *A. myosuroides* was investigated. In this chapter, the traits are evaluated for their contribution to suppressive ability under different, agronomically-relevant scenarios. The interaction between cultivar choice and two common strategies for controlling *A. myosuroides*, sowing density and delayed drilling, is examined. In addition, suppression of a second weed species *S. media* (common chickweed) by wheat cultivars is investigated, to determine if the traits related to its suppression are the same as those that suppress *A. myosuroides*.

5.1.1 The role of crop density

Decreased weed biomass and seed return has been observed when a crop stand is sown at higher density, and is associated with suppression of weed growth (Lutman *et al.*, 2013). A high density crop stand results in increased dominance of the canopy by the crop. With the crop claiming a greater share of the canopy, giving it an asymmetric advantage, and weeds are thus deprived of light and their growth is limited (Weiner *et al.*, 2001). It is a weed management strategy that is low risk and low cost to implement. Within the UK, employing higher seed rates is already a popular strategy in winter wheat, with average values of 300-350 seeds m^2 and, in some cases, exceeding 500 seeds m^2. Of these seeds, on average 67% would be expected to establish (Blake *et al.*, 2003). The relationship between crop density and yield loss or weed seed

return is non-linear. It behaves under the principal of diminishing returns, with the incremental benefit of increased crop density decreasing as intraspecific crop competition increases.

Studies have reported that increased sowing rate and cultivar choice complement one another, with all cultivars benefitting from an increase in crop density (Grundy *et al.*, 1997; Lemerle *et al.*, 1996; O'Donovan *et al.*, 2000). However, some studies have suggested that there is no discernible benefit to sowing some cultivars at a higher density (Korres & Froud-Williams, 2002). Increasing density has also been shown to increase grain yield in the presence of weeds, though this is not ubiquitous across sites (Paynter & Hills, 2009; O'Donovan *et al.*, 2000). Given the preference for higher seeding densities within UK arable agriculture as a means of weed seed-bank management, an understanding of if, and how, potential target traits interact with stand density could help refine the efforts of breeders. In addition, if cultivars do not benefit equally from an increased sowing density, understanding the traits that underlie this interaction would be valuable. For example, it is possible that the differences between cultivars become less important in light capture when a crop is sown at higher rates.

5.1.2 The role of delayed drilling

Delayed drilling is an effective method to reduce *Alopecurus myosuroides* numbers in a winter cereal. The primary germination window for *A. myosuroides* is September and early October, with a small flush common in the spring (Colbach *et al.*, 2007). To delay the sowing of a winter cereal into late October or November will reduce the opportunity for *A. myosuroides* to emerge within the crop (Lutman *et al.*, 2013). It has also been reported that *A. myosuroides* has reduced

competitive ability in a late-drilled winter wheat crop (Melander, 1995).

Commercial cultivars often come with advice on how appropriate they are for delayed drilling. But little is known about how cultivar choice and competitive traits interact with delayed drilling. However, potential competitive traits have been noted to be influenced by drilling date (Cosser *et al.*, 1997; Rebetzke & Richards, 1999). As such, cultivar suppressive performance and trait interactions with drilling date deserve further investigation in order to maximise weed management strategies.

5.1.3 Broadly-suppressive or species-specific?

Studies into suppression often focus on a single weed species known to be problematic to the target crop in a given region, or an entire weed assemblage. Whilst this is a practical approach, knowledge on whether a cultivar and suppressive traits ubiquitously impact numerous weed species or has a species-specific impact would be valuable. If cultivars were shown to be 'broadly-suppressive', they would be more valuable where the control of multiple weed species is required.

Previous work has shown that weed species differ in their response to cultivars, with shorter cultivars being poorer suppressors of upright weeds such as *Avena fatua* (L.) whilst *Veronica hederifolia* (L.) appears to benefit under taller cultivars (Gooding *et al.*, 1993). In a study with multiple weeds, taller species *Apera spica-venti* (L.) was most greatly impacted by taller cultivars (Drews *et al.*, 2009). Clarifying if the suppressive ability of wheat cultivars varies between weed species will be valuable to a farmer, allowing them to target weed species more appropriately.

5.2 Aims

In this chapter, the following hypotheses will be tested.

1. Variation in suppression of *A. myosuroides* between cultivars and the traits related to suppressive ability will be consistent at two crop densities.
2. Variation in suppression and tolerance of *A. myosuroides* between cultivars, and the traits related, will be consistent at two drilling dates.
3. Variation in suppression between cultivars and the traits related to suppressive ability against *A. myosuroides* will also be similar when competing with another weed species, *Stellaria media*.

5.3 Materials and methods

5.3.1 Cultivar and weed choice

Twelve cultivars were investigated (10 wheat, one barley, one oat). Details regarding their selection can be found in section 2.3.1.1. Due to the difficulties of managing different crop species within a single experiment, only wheat cultivars were included in the drill date field experiment. *Stellaria media* (L.) was selected as the weed species for comparison in the species-specificity experiment. *Stellaria media* is an annual, prostrate plant that germinates throughout the year and is particularly problematic in the organic sector. Due to its ability to grow at low temperatures, it may smother a crop whilst it is overwintering (Clarke *et al.*, 2010). It was included to ascertain if traits that determine competitive success over *A. myosuroides* will have the same impact on a weed species with a different morphology.

5.3.2 Crop stand density experiment

The crop stand density experiment was conducted in the 2013-14 growing season in containers arranged in a randomised block design on outdoor sand-beds. Pre-germination and sowing of *A. myosuroides*, and sowing of the wheat cultivars, followed the same method as described for 2013-14 in section 3.3.2. In addition to the standard density of wheat and *A. myosuroides* described in Chapter Three (herein referred to as the 'high density' treatment), a low crop density treatment was added to the experiment and replicated three times. In these, the crop was planted at half the density of the 'high density' containers (Figures 5.1 and 5.2). Further information on crop and *A. myosuroides* density are presented in Table 5.1. The two contrasting densities were expected to have a strong impact on *A. myosuroides* seed return. With high seeding rates in the UK rarely exceeding 500 seeds m^{-2}, and with approximately 67% of seeds expected to establish (Blake *et al.*, 2003), the 'high density' used in this experiment provide a reasonable representation of those in the field.

Data on cultivar emergence, early leaf parameters, early leaf counts and angle (higher values denoting more planophile leaves), spike emergence, continuous stem counts, height, flag leaf dimensions and thousand grain weight (TGW) were collected. These traits, and measures of *A. myosuroides* fitness, were recorded as described for 2013-14 in section 2.3.1. Traits from the ecophysiological experiment were also included in analysis. These were LAR, RWR, SLA, LWR, ABGW, RGR_{GA}, RGR_{W} and early green area. Values were applied to both experimental treatments. The description of their collection and calculation can be found in section 2.3.1.

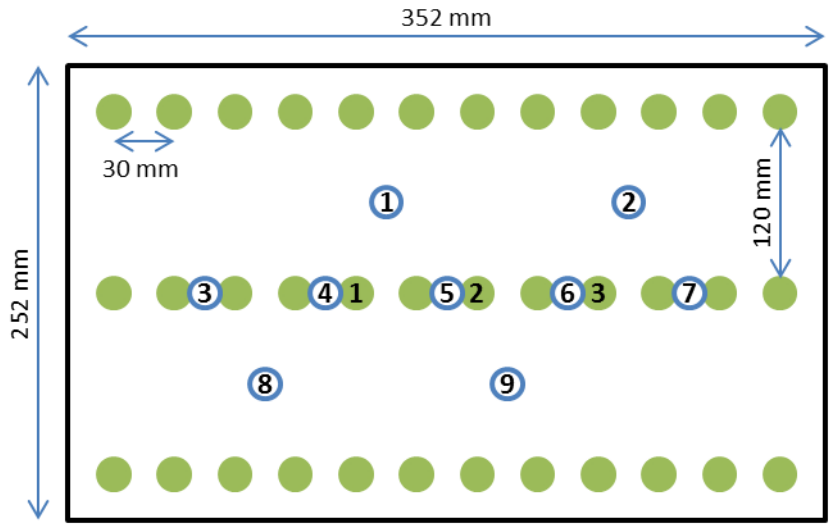

Figure 5.1 - Arrangement of cultivars and weed individuals in high-density experimental containers, with sampled individuals numbered. • are cultivars, o are *A. myosuroides*. Weed density 98.4 m^{-2}, crop density 393.5 m^{-2} (container)/276.4 m^{-2} (field equivalent)

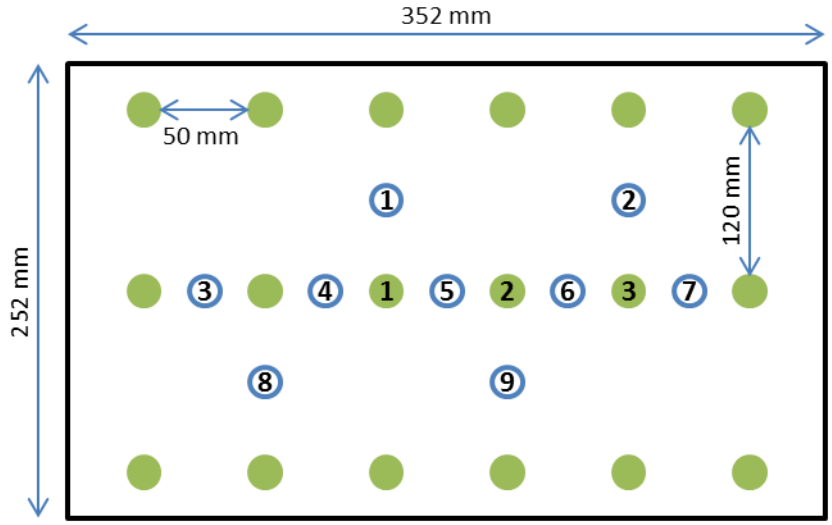

Figure 5.2 - Arrangement of cultivar and weed individuals in low-density experimental containers, with sampled individuals numbered. • = cultivars, o = *A. myosuroides*. Weed density 98.4 m^{-2}, crop density 196.7 m^{-2} (container)/117.9 m^{-2} (field equivalent)

Table 5.1 - The crop stand density used in 'high' and 'low' density treatments. As the experiment was conducted in containers on outdoor sand-beds, cultivar density is presented as 'by container' basis, and 'by field' to translate the sowing pattern to the field. Sown 15-17 October 2013.

	Container dimensions (mm)	Crop density (by field equivalent) (m^{-2})	Crop density (by containers) (m^{-2})	Weed density (by containers) (m^{-2})
High density	257 x 356 x 162	276.39	393.48	98.4
Low density	257 x 356 x 162	117.86	196.74	98.4

5.3.3 Delayed drilling experiment

The delayed drilling experiment was conducted in the field at Rothamsted Research, UK in 2013-14. A split-split plot design was used with randomisation by Genstat 14, with replicate the highest level of organisation, followed by drilling date. Plots were split into subplots, sown with *A. myosuroides* ('weedy') and without ('weed-free'). Though a drilling date experiment was planned for 2012-13, poor weather meant that the second date could not be drilled.

The 'early' plots were drilled on 4 October 2013 and 'late' plots were drilled on 24 October 2013. Early sowing in the UK is often in the first half of September, but it was not possible to drill the early date prior to 4 October. The early date was drilled at 350 seeds m^{-2}, and the later date was drilled at 400 seeds m^{-2}, to account for lower expected germination at lower temperatures. The aim was to achieve an equivalent *A. myosuroides* density of 25 to 100 plants m^{-2} in both early and late drilled plots. Germination of *A. myosuroides* is restricted at low temperatures, so a higher volume of seed was sown on the later drilling date. It was decided that 13.5g of *A. myosuroides* seed should be sown per 'weedy' subplot on the early drilling date,

and increased to 15g for the late drilling date to account for lower temperatures. Crop and *A. myosuroides* density was counted as described in section 4.3.4.2. Dates of density counts, as well as other experimental procedures, can be found in Table 5.2.

Table 5.2 - The dates of experimental procedures in both drill conditions

Experimental procedure	Early drill treatment	Late drill treatment
Sowing date	4 Oct 2013	24 Oct 2013
Wheat density counts	26 Oct 20113	6 Dec 2013
A. myo density counts	5 March 2014	
Sampling for early vigour	21 Jan 2014 Began	19 Feb 2014 Began
Stem counts/crop height	29 Oct 2013	25 Nov 2013
Early height	25 Nov 2013	8 Jan 2014
Leaf counts	21 Jan 2014	19 Feb 2014
Biomass harvest	25 June - 10 July 2014	
Grain harvest	19-20 Aug 2014	

5.3.3.1 *Early vigour traits*

Ten wheat individuals were randomly selected and removed from each plot at ground level, ensuring the entirety of aboveground growth was taken. Time of collection across the two drilling dates corresponded with when the crop was at approximate growth stage 23 to 25. Material was collected on January 21 and February 19 2014 for the early and late drilled plots, respectively. The material collected was used to calculate early aboveground weight (ABGW), green area, leaf area and specific leaf area (SLA). The methods for determining these traits are described in section 2.3.1.3.

5.3.3.2 *Early leaf counts and parameters*

Leaf counts were taken on 21 January and 19 February 2014 for early and late drilling dates, respectively. An average of 10 individuals were taken. Early leaf length and width

measurements could not be collected from the plots due to time constraints.

5.3.3.3 *Height and tiller production*

Measurements of height and tiller production were as described for the 2013-14 experiment described in section 4.3.4.4. Early cultivar height was determined from 185.5 ptt (25 November 2013) in the early drilled plots and 172.5 ptt (8 January 2014) in the late drilled plots. These time points were chosen as they would represent similar developmental time points between the two drilling dates, and were similar to photothermal time points from which early height was quantified in the sand-bed based experiments.

5.3.3.4 *Biomass harvest*

Fitness of *A. myosuroides* (measured as biomass and seed return) and the cultivar ear index were measured as described in section 4.3.4.6.

5.3.3.5 *Flag leaf parameters*

Flag leaf angle, length, width, area and SLA were measured as described in section 4.3.4.7.

5.3.4 Weed species specificity experiment

The comparison of suppression of *A. myosuroides* and *S. media* was conducted 2012-13 using the sand-bed-based container method, with wheat and *A. myosuroides* sown and arranged as described in section 3.3.2.. *Stellaria media* was pre-germinated as described for *A. myosuroides*, although *S.media* seeds were soaked in 3.5 ml of potassium nitrate solution instead of 5.5 ml to account for their smaller seed size.

Emergence of the wheat cultivars was poor in the 2012-13 sand-beds experiment and individuals could not always be

supplemented with spares. Containers that had fewer than 34 of the desired 36 were excluded from the study. *Alopecurus myosuroides* containers were prioritised for spares because these were required for comparisons across the years (for the experiment for Chapter Three). As a result, Gallant, Gerald, Volume and replicate three of Conqueror were removed from the *S. media* treatment.

5.3.4.1 *Data collection*

Data was collected on wheat emergence time, tiller production and height over time, leaf parameters, spike emergence and *A. myosuroides* fitness following the descriptions as given in section 3.3.3. Ecophysiological traits from the experiment described in Chapter Two were included, with each value per cultivar applied to both weed treatments.

In the spring, *S. media* leafy growth began to extend beyond the containers and escape light competition (Figure 5.3). After initially attempting to limit *S. media* escape by placing fine meshing around the containers at a height of 20cm, *S. media* was harvested on May 13 and 14, 2013. Wheat was not removed from containers, allowing for maturity traits to be quantified, although these will be treated with caution in the analysis. Biomass was the sole measure of fitness for *S. media*, owing to the high numbers of reproductive structures and difficulties in effective subsampling.

Figure 5.3 - Weed species *S. media* growing in a container alongside cultivar Robigus. Taken 10 May 2013. *Stellaria media* was harvested on 13-14 May, to reduce the influence of escape from light competition on fitness measures.

5.3.5 Statistical analysis

Comparisons between *A. myosuroides* seed return in contrasting treatments were conducted using a two way ANOVA in Genstat 16 with a Bonferroni test of multiple comparisons. Both the delayed sowing experiment and the density experiment underwent factorial ANOVA to investigate the interaction between cultivar and drill date / density. Seed return and % yield loss in the delayed sowing experiment underwent square root transformation to correct for normality prior to ANOVA. In the weed specificity experiment, *A. myosuroides* and *S. media* returned different average dry weights, owing to the size differences of these species. It was necessary to make the response of each species to cultivar comparable. To do this, the reported biomasses for each weed species was standardized by zero. This involved calculating the mean for each species and

deriving the difference from zero for each individual sample. This gave values for each species a zero mean whilst maintaining the variability necessary for seeking differences in the suppressive impact of the cultivars.

5.3.5.1 *Modelling height growth and stem number*

Cultivar tiller production was modelled using a split-line plot (see section 3.3.5.4) and height growth modelled using an unconstrained generalized logistic model (see section 3.3.5.3). Due to the early harvest of *S. media*, it was decided not to include tillering parameters in the weed specificity analysis. The sudden removal of the weed competitor would have influenced the values, or made their relevance to competitive outcomes obsolete.

5.3.5.2 *Correlation analysis and PCA*

In each experiment, a Pearson's correlation was conducted separately for each treatment. Relationships between cultivar traits and the seed return (and, in the drilling date experiment, % yield loss) were of interest.

Principal component analysis (PCA) was used to examine the occurrence of traits into groups that explained the differences between the cultivars in the study. Cultivar scores along PCs 1 and 2 were regressed against weed seed return (and, in the drilling date experiment, % yield loss) to ascertain if the PCs were composed of a suite of traits that may be considered competitive.

5.3.5.3 *LMM for container-based experiment*

Due to the unbalanced nature of the data and instances of non-orthogonality, LMM analyses were employed to seek traits that predicted suppressive and tolerance ability. The LMM was able to account for the randomised complete block design, and there

was limited variability between the three block structures. Data composing the y variate in the density (*A. myosuroides* seed return) was normalised via a logarithmic transformation. After standardization by zero to account for differences in biomass between *A. myosuroides* and *S. media*, and residuals were suitable for the LMM.

The full model was run in each experiment. For a backwards elimination model, terms were individually dropped in order of least significance until all terms remaining were within statistical significance.

5.3.5.4 *LMM in field data*

In the analysis focussing on suppressive traits, *A. myosuroides* seed return was the y variate. The residuals were adequate for no required data transformation. In the analysis of tolerance traits, a logit transformation was necessary, owing to the tolerance being expressed as a percentage.

Suppression and tolerance experiments conducted in the field were of a split-plot design, which is difficult to implement in Genstat LMM analysis. There was low variability between the blocks relative to plots, which justified accounting for structure by merging the block and whole-plot strata into one. This results in Genstat treating the design as having 6 blocks, to which differing drill dates were applied. Plots and subplots within blocks are still recognised as being of a split-plot structure.

Non-convergence was observed, which may have been caused by a low number of blocks with which to estimate variation, and was accounted for by making the iteration thresholds less strict. This allowed the model to make sensible predictions.

The full model was run in each experiment. For a backwards elimination model, terms were individually dropped in order of least significance until all terms remaining were within statistical significance.

5.4 **Results**

5.4.1 Sowing density

Cultivars achieved differing levels of suppression of *A. myosuroides*, ($P<0.001$; 11 d.f.), and *A. myosuroides* seed return was lower under high density ($P<0.001$; 1 d.f.). There was no interaction between density and cultivar (Figure 5.4). Output of a correlation analysis shows that cultivars that were suppressive at higher densities were also suppressive at lower densities ($r=0.7987$; $P=0.0018$) (Figure 5.5). According to the Bonferroni multiple comparisons test, the differences were most apparent when comparing between species. In wheat cultivars, significant differences in suppressive ability were restricted to cultivars at the extremes (Duxford, Robigus and Conqueror, the three most suppressive cultivars, were significantly more suppressive than KWS Santiago, the poorest performer).

Numerous cultivar traits were associated with changes in *A. myosuroides* seed return at high density, including TGW, early green area and % stem loss. However, none of these traits was correlated with *A. myosuroides* seed return in a low density stand (Table 5.3). Net assimilation rate during seedling establishment was the only trait associated with *A. myosuroides* seed return in the low density stand. This correlation was not observed in the high density stand (Table 5.3).

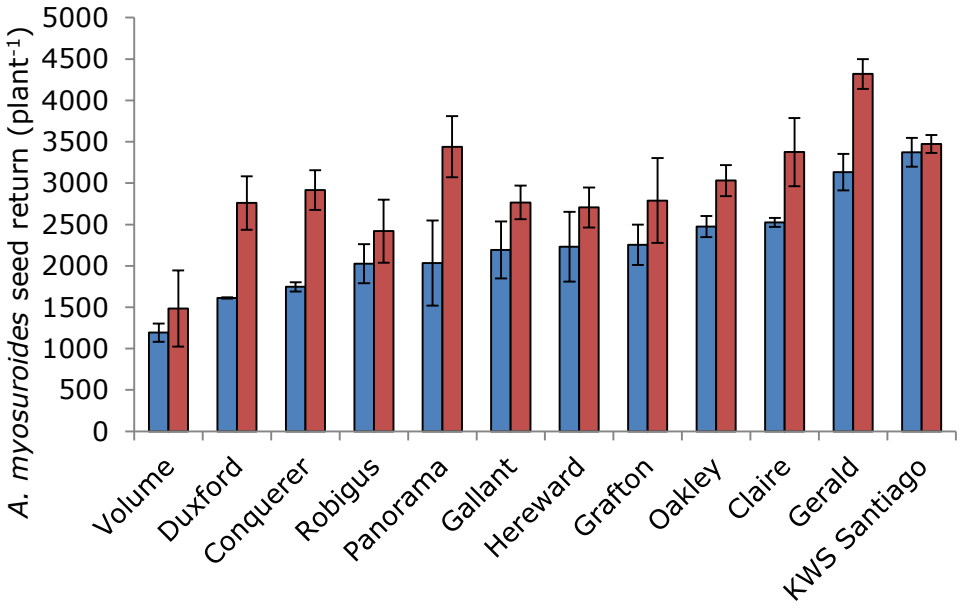

Figure 5.4 - The seed return (plant^{-1}) of *A. myosuroides* when grown in competition with cultivars at different densities, with s.e. bars. All cultivars are wheat, bar Volume (barley) and Gerald (Oat). Ordered by seed return under high density. ■ =High density ■ = Low density

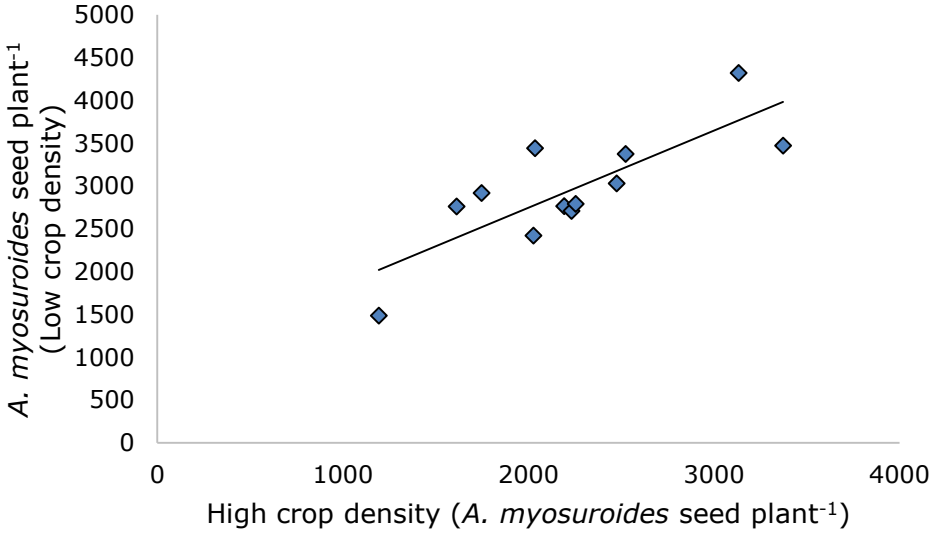

Figure 5.5 - The relationship between the seed return (plant^{-1}) of *A. myosuroides* by different cultivars at high and low sowing densities.

Table 5.3 - Correlation coefficients of wheat traits in relation to seed production of *A. myosuroides*, when crop stand is at different densities. * = P<0.05; ** = P<0.01. Significant correlations were evident for the same traits in both densities when barley cultivar Volume and oat cultivar Gerald were included in the analysis (data not shown). Leaf angle was measured with larger values indicating more planophile leaves.

Cultivar traits	Seed return	
	High density	Low density
TGW	**0.5706****	0.3037
50% emergence	0.0545	0.2554
75% spike emergence	**0.4419***	0.2049
ABGW	-0.2269	-0.0583
% stem loss	**0.4906****	0.036
Early green area	**-0.5024****	0.0863
Early height	-0.3793	-0.1039
Early leaf angle	**0.522****	-0.0449
Early leaf counts	0.1905	-0.1634
Early leaf length	-0.1894	0.1087
Early leaf width	**-0.4129***	0.0261
Final height	0.0306	0.2035
Final stem count	-0.3492	-0.0999
Flag leaf SLA	0.1683	-0.164
Flag leaf angle	0.0945	0.0679
Flag leaf area	0.159	0.2577
Flag leaf length	0.1278	0.2463
Flag leaf width	-0.021	-0.0506
Maximum stem number	**0.5573****	-0.1015
LAR	**-0.5228****	-0.1517
LWR	-0.1129	-0.3379
Max. growth rate	0.3798	0.1625
NAR	0.1919	**0.395***
RGR_W	-0.2383	0.2913
RGR_{GA}	-0.1451	0.2797
RWR	0.0615	-0.0484
SLA	-0.3693	-0.007
Rate of tillering	0.2775	-0.1805
Time of max. growth rate	0.2892	-0.2893
Time of max. stem number	0.2356	0.1588

In both PCAs, PC1 was highly loaded for traits associated with early growth (early leaf parameters, early green area, early height) and timing of maturity (such as time of maximum stem number and time of 75% spike emergence) (Figures 5.6 and 5.7). Traits associated with early green area and height have

been used as indicators of early vigour. As such, PC1 could be said to be driven by cultivar developmental rate. There was no significant relationship between cultivar scores for PC1 or 2 and *A. myosuroides* seed return at both densities, indicating that neither PC could be considered a competitive suite of traits.

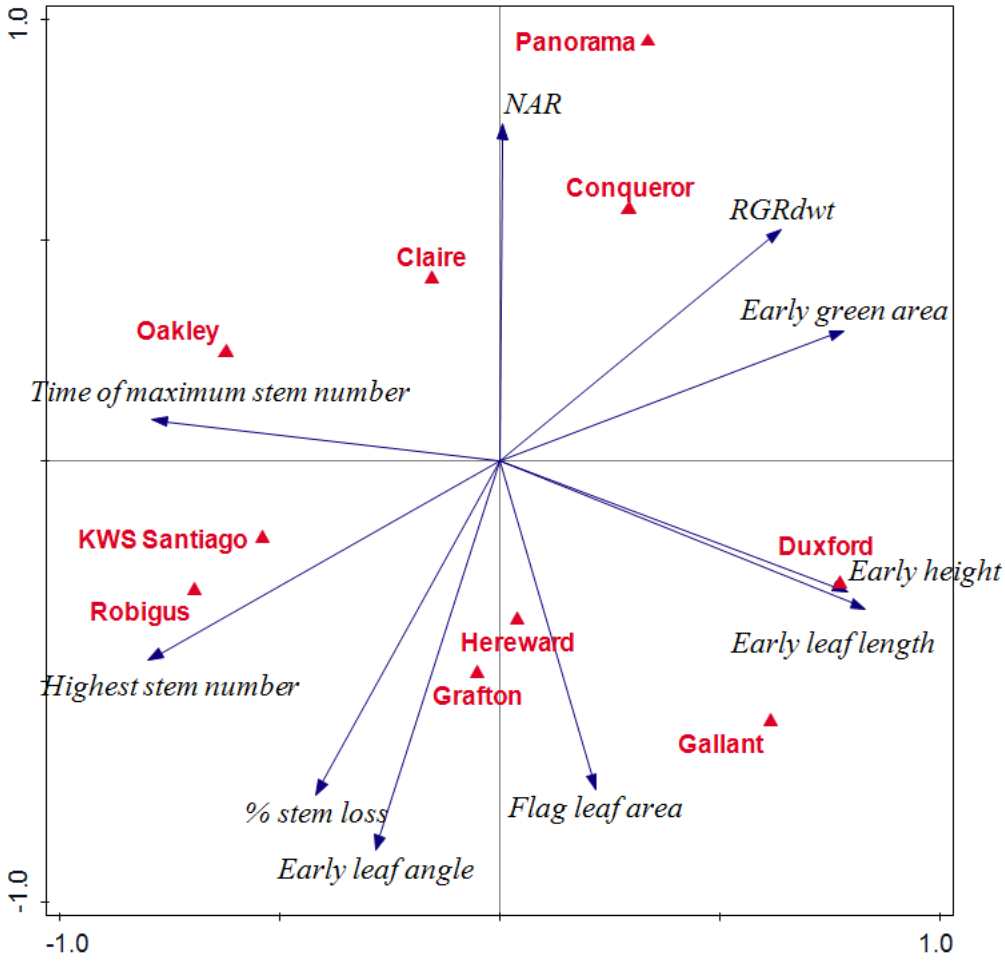

Figure 5.6 - Principal Components Analysis for high density stands of wheat cultivars. Percentage variance accounted for by the two axes = 49.79% (PC1 = 28.11%, PC2 = 21.68%). Only the 10 traits with the highest loadings are shown.

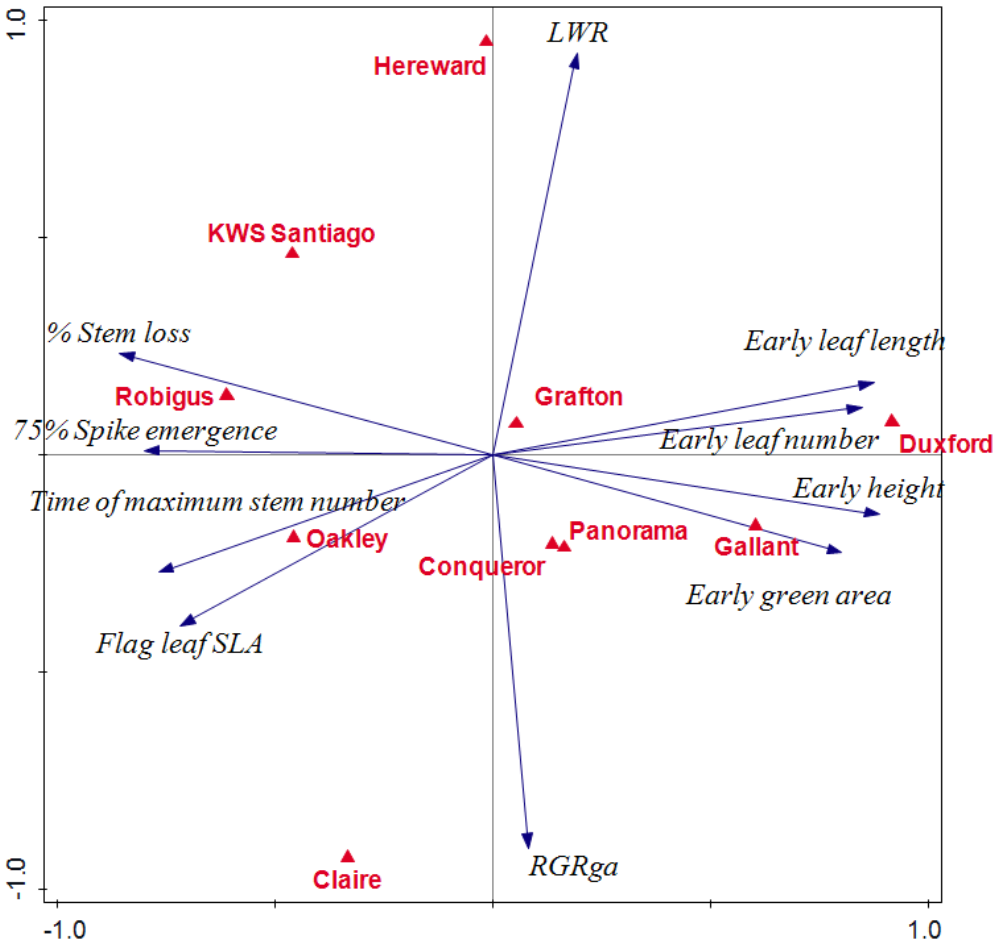

Figure 5.7 - Principal Components Analysis for low density stands of wheat cultivars. Percentage variance accounted for by the two axes = 49.95% (PC1 = 34.13%, PC2 = 15.82%). Only the 10 traits with the highest loadings are shown

Density was a key driver of the LMM, with a lower crop stand permitting high weed seed return throughout the experiment. When terms were sequentially dropped from the model, later spike emergence was related to increased *A. myosuroides* seed return in both densities. A greater maximum stem number was related to greater *A. myosuroides* seed return, but only in the high density treatment (Table 5.4).

Table 5.4 - LMM traits indicated as predictors of suppression of *A. myosuroides* under two crop densities.

Fixed term	Wald statistic	n.d.f.	F statistic	d.d.f.	F pr
Sequentially adding terms to fixed model					
Maximum stem number	17.81	1	17.81	54	<0.001
75% spike emergence	5.93	1	5.93	54	0.018
Density	20.24	1	20.24	54	<0.001
Maximum stem number x Density	9.5	1	9.5	54	0.003
Dropping individual terms from full fixed model					
75% spike emergence	8.38	1	8.38	54	0.005
Maximum stem number x Density	9.5	1	9.5	54	0.003

5.4.2 Drilling date

Cultivars in the field were present in densities of 281 ± 9.07 plants m^{-2} in the early drilling date and 320.5 ± 10.58 plants m^{-2} in the late drilling date. The *A. myosuroides* in the 'weedy' subplots was present in densities of 23.3 ± 0.76 plants m^{-2} in the early drilling date and 9.8 ± 2.81 plants m^{-2} in the late drilling date.

No difference in suppressive ability was noted between cultivars when both drilling dates were considered together (P=0.87; 9 d.f.) (Figure 5.8). Seed return differed between the two drilling dates (P<0.001; 1 d.f.), with *A. myosuroides* individuals in the late drilled plots producing an mean 3456 ± 453.3 seeds, whilst those in the early-drilled plots produced 7252 ± 211 seeds per plant. However, there was no indication of an interaction between cultivar suppressive ability and drilling date (P=0.205; 9 d.f.). When years were analysed separately, suppressive differences were apparent in cultivars when drilled on 24 October (P=0.032; 9 d.f.), though were restricted to the strongest (Gallant) and poorest (Claire) suppressors. However, no differences in cultivar suppressive ability were apparent in

the early drilled plots (P=0.96; 9 d.f.). Seed return of *A. myosuroides* in early and late-drilled cultivars was negatively correlated, just short of significance (-0.6069; P=0.0628), implying there may be a trade-off between suppressive strength at different drilling dates (Figure 5.9). The outlier is Claire, which saw equivalent *A. myosuroides* seed return at both drill dates. When Claire is removed, the correlation becomes statistically significant (r=-0.7061; P=0.0335).

No difference in cultivar tolerance was found (P=0.256; d.f. 9), but there was a significant difference between drilling dates (P<0.001; d.f. 1), with early drilled cultivars suffering a % yield loss of 2.5 ± 0.116 per *A. myosuroides* individual and late drilling resulting in a % yield loss of 2.0 ± 0.155 per individual. In addition, there was a significant interaction between cultivar and drilling date (P=0.004; d.f. 9) (Figure 5.10), with no difference between cultivars in the early drilling date (P=0.175; d.f. 9), but significant differences in the late drilled plots (P=0.039; d.f. 9). The Bonferroni multiple comparisons test reported that this difference was restricted to the strongest (Panorama) and poorest (Claire) performers. Claire, which drove the interaction between drill date and cultivar tolerance, is acknowledged by the arable industry as better suited to early sowing due to its slow developmental speed. This suggests that Claire is more prone to yield loss through *A. myosuroides* competition, as the weed is able to establish and acquire resources at a quicker rate than Claire early in the season, thus acquiring an increasingly disproportionate share of resources.

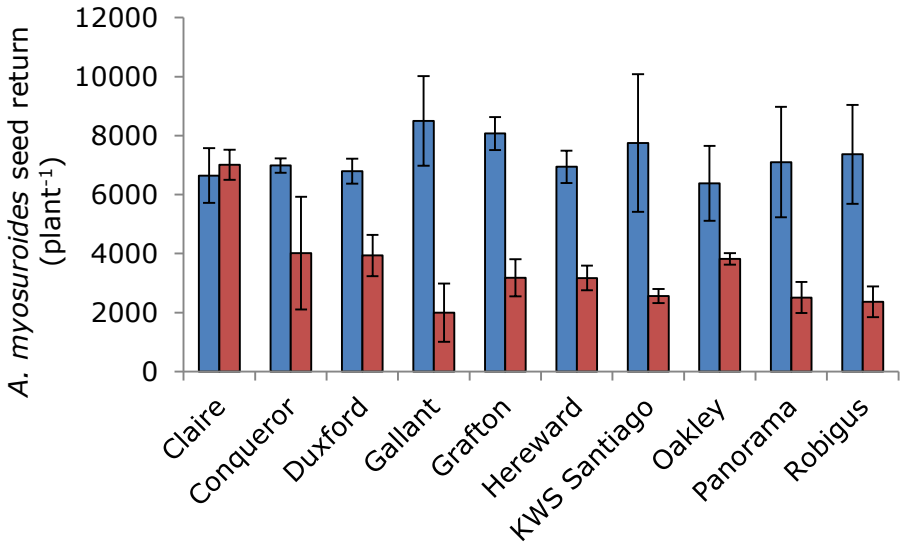

Figure 5.8 - The seed return of *A. myosuroides* (plant^{-1}) when grown in competition at different drilling dates, with s.e. bars. All cultivars are wheat. ■ =Drilled 4 October 2013 (Early drilled); ■ = Drilled 24 October 2013 (Late drilled)

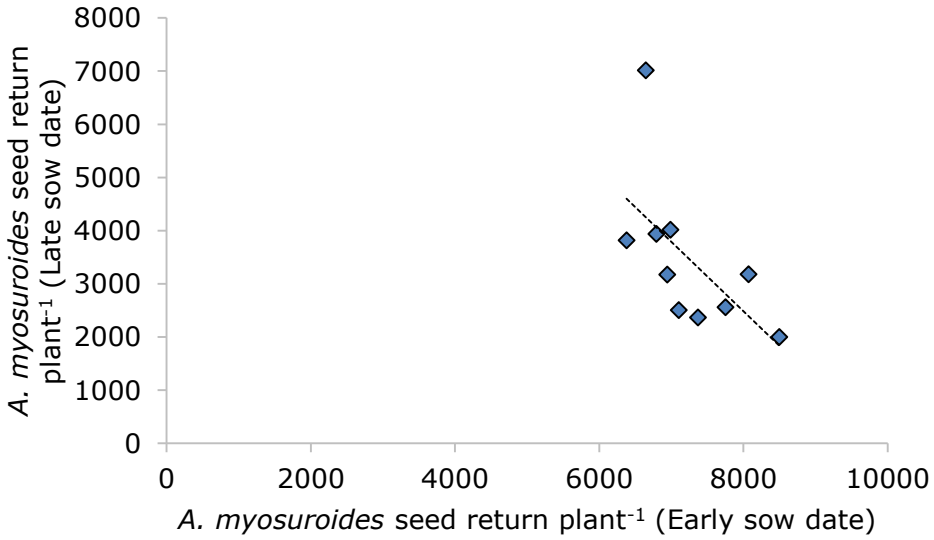

Figure 5.9 - The relationship between the seed return of *A. myosuroides* (plant^{-1}) by different cultivars at early and late sowing dates. The correlation becomes statistically significant when the outlier (Claire) is removed.

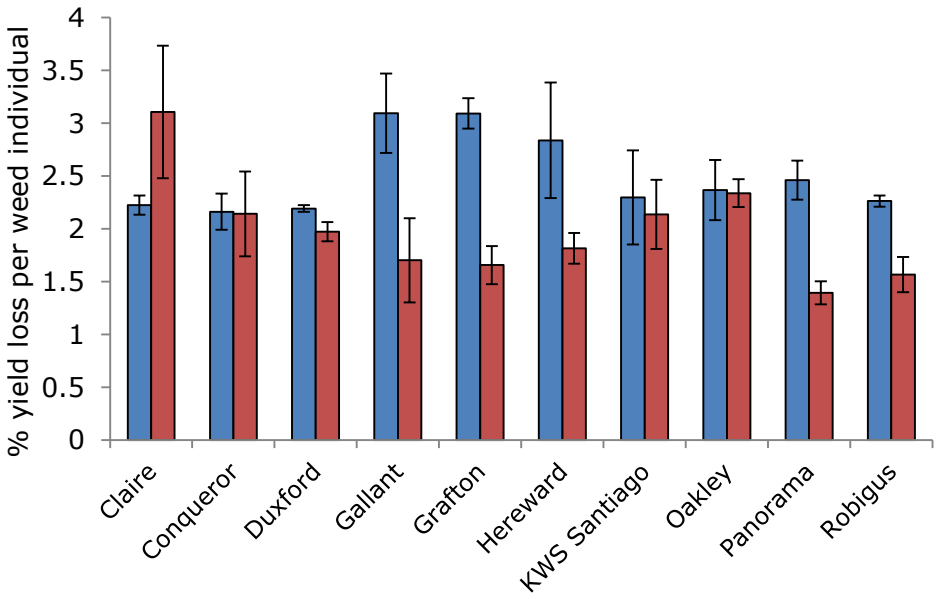

Figure 5.10 - The % yield loss per *A. myosuroides* individual, to account for density, with s.e. bars. All cultivars are wheat. ■ =Drilled 4 October 2013 (Early drilled); ■ = Drilled 24 October 2013 (Late drilled)

Seed return of *A. myosuroides* was associated with early season traits in early drilling dates, such as ABGW and green area. In the late drilling date, final stem count was correlated with seed return (Table 5.5). This suggests that, when a wheat crop is sown later, competition around the period of ear emergence to grain filling becomes more important. Final stem count was related to tolerance at both drilling dates, likely due to its relationship to yield. However, the relationship switches from negative to positive between the early and late drill date. Understanding the importance of potentially competitive traits that are present at later growth stages can be difficult. They may not be directly competitive – rather, they may be the result of earlier suppression, which has allowed the cultivar to acquire a greater share of resources at later developmental stage.

The trait loadings along PC1 and 2 were not consistent between the two drilling dates. There was an exception in traits associated with early green area, which were present in PC1 in

both drilling dates (Figures 5.11 and 5.12). There was no significant relationship between PC scores of PC1 or 2 and *A. myosuroides* seed return or tolerance, suggesting that the PCs did not constitute a 'competitive' suite of traits

Table 5.5 – Correlation coefficients of wheat traits in relation to seed production of *A. myosuroides* and yield retention in the presence of *A. myosuroides*. * = P<0.05; ** = P<0.01; n=30.

	Seed return		Tolerance	
Cultivar traits	Early drill	Late drill	Early drill	Late drill
TGW	-0.0949	-0.1459	0.0585	0.2413
ABGW	**0.5466****	-0.1155	-0.2045	0.4327
Early height	0.2143	-0.2009	-0.345	0.2859
Final stem count	0.2959	**-0.6165****	**-0.3995***	**0.5287***
Flag leaf SLA	0.027	-0.0061	0.1886	-0.037
Flag leaf angle	-0.0399	0.0932	0.2163	-0.2071
Flag leaf length	0.063	-0.3319	-0.1538	0.2945
Flag leaf width	0.0543	-0.2025	0.1084	0.1619
Final height	0.1559	-0.2611	0.1305	0.0106
Maximum stem number	0.2181	0.0803	-0.0223	-0.1103
Early leaf area	**0.4501***	0.0794	-0.1216	0.0841
Early leaf number	**0.4968****	-0.1865	-0.1851	0.2917
Time of max. stem number	-0.1859	0.2442	0.2157	-0.2632
Rate of tillering	0.321	-0.2321	-0.2565	0.2258
Early SLA	0.0945	0.1721	0.122	-0.1277
Early green area	**0.4708****	0.0682	-0.1482	0.0871
% stem loss	-0.0635	0.3838	0.2851	-0.3644
Flag leaf area	-0.0635	-0.0735	-0.2577	-0.0268
Ear index	-0.2469	-0.0756	-0.3116	-0.0735
Time of max. growth rate	0.0426	-0.2986	-0.1258	0.3556

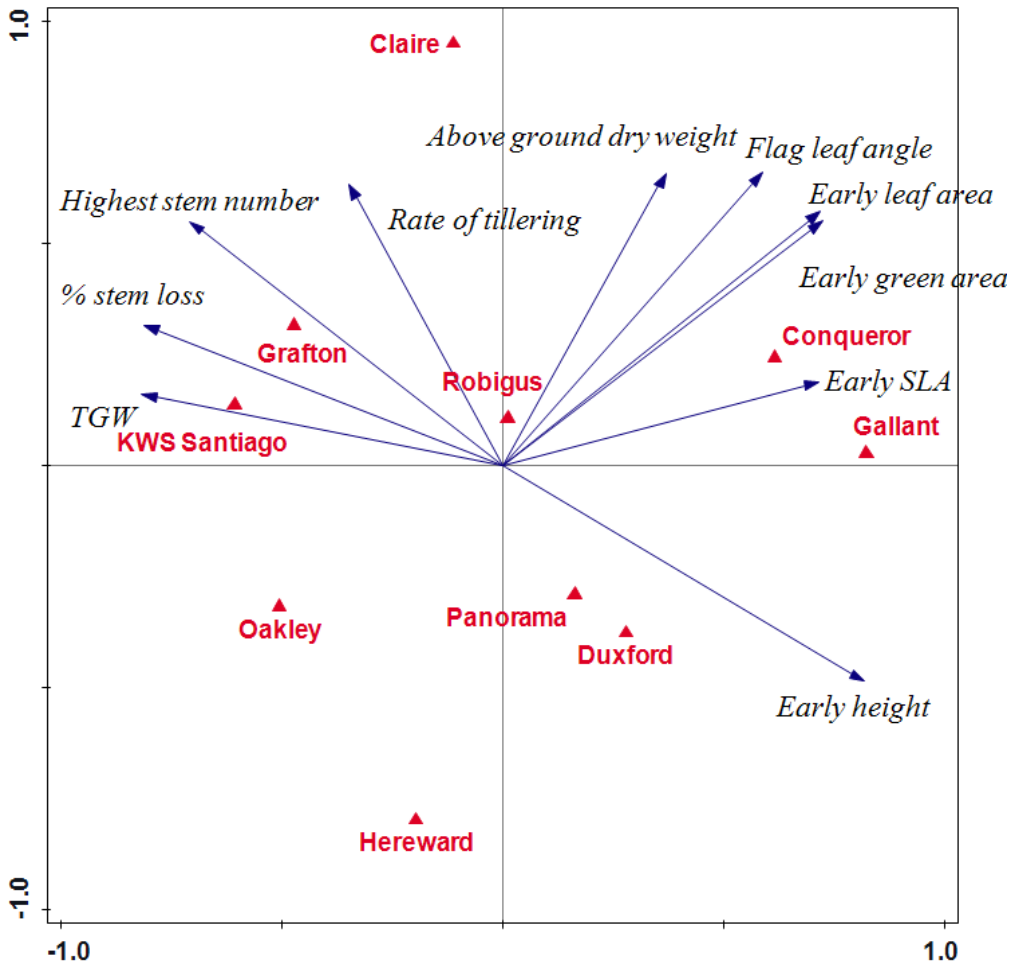

Figure 5.11 - Principal Component Analysis of traits in early drilled plots. Percentage variance accounted for = 46.89% (PC1 = 27.15%, PC2 = 19.74%). Only the 10 traits with the highest loadings are shown.

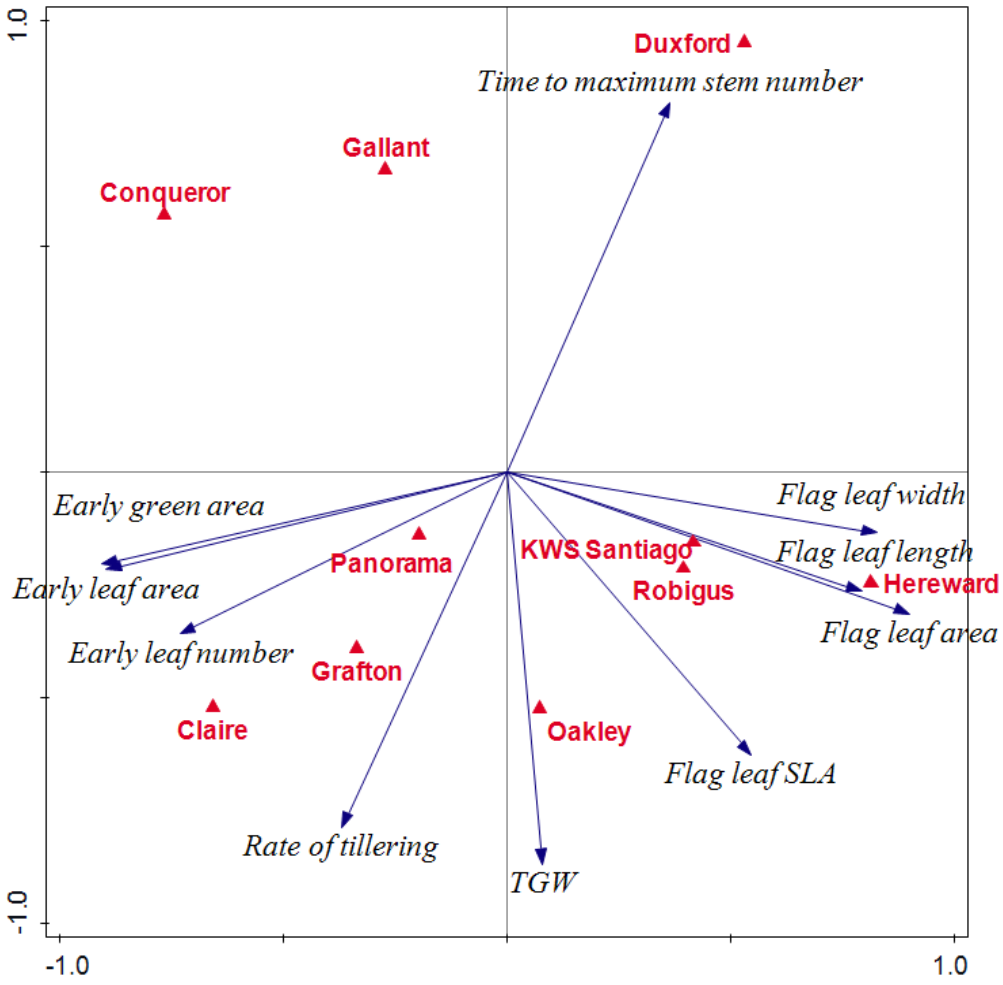

Figure 5.12 - Principal Component Analysis of traits in late drilled plots. Percentage variance accounted for = 57.16% (PC1 = 33.2%, PC2 = 23.96%). Only the 10 traits with the highest loadings are shown.

Linear mixed modelling identified ABGW and early leaf area as a predictors of cultivar suppressive ability, and in the late drill a lower maximum stem number was related to reduced *A. myosuroides* seed return. Drill date has the greatest impact on *A. myosuroides* seed return (Table 5.6). No traits were found to be sufficient predictors of tolerance.

Table 5.6 - L output for traits in wheat suppressive against *A. myosuroides* across two drilling dates.

Fixed term	Wald statistic	n.d.f.	F statistic	d.d.f.	F pr
Sequentially adding terms to fixed model					
Final stem number	5.26	1	5.26	51	0.026
ABGW	31.98	1	31.98	50.2	<0.001
Early leaf area	1.08	1	1.08	49.2	0.303
Drill date	4.84	1	4.84	11.2	0.05
Final stem number x drill date	4.23	1	4.23	50.8	0.045
Dropping individual terms from full fixed model					
ABGW	11.88	1	11.88	50.2	0.001
Early leaf area	4.86	1	4.86	49.2	0.032
Final stem count x drill date	4.23	1	4.23	50.8	0.045

5.4.3 Weed species specificity

ANOVA reported no significant difference in the suppressive ability the cultivars (P=0.144; d.f. 9) or the ability of cultivars to suppress the two weed species (P=0.818; d.f. 1) (Figure 5.13). There was no discernible relationship in the ability of cultivars to suppress *A. myosuroides* or *S. media* (r=0.3741; P=0.3212), but without differences between cultivars observed it is not possible to remark on how suppressive ranking of cultivars will differ according to weed species (Figure 5.14).

There was evidence that % stem loss was positively correlated with mature biomass of *A. myosuroides* (Table 5.7). Percentage stem loss was not available for the *S. media* treatment, so no conclusion can be drawn about this trait and if any competitive interaction is specific to *A. myosuroides* or also relevant in competition with *S. media*. Greater flag leaf area was associated with increased *S. media* biomass, but no association was found in *A. myosuroides* (Table 5.7). However, flag leaf area was measured several weeks after the harvesting of *S. media*, so this result must be considered with due caution. The LMM

analysis did not identify any traits of importance in determining the suppressive ability of wheat cultivars against either *A. myosuroides* or *S. media*.

Traits associated with stems were not available for the PCA of cultivar traits in the *S. media* treatment, and this will have influenced the loadings of traits along PCs 1 and 2. However, in both weed species treatments, early green area, early height and early leaf width were highly loaded, and stem traits were not drivers of PC1 for the *A. myosuroides* treatment (Figures 5.15 and 5.16). All PC1 traits were associated with the earlier phases of growth, having been acquired from autumn measurements in containers or from the destructive ecophysiological traits experiment. The ecophysiological traits need to be considered with caution, as the same values were applied to both weed-specificity treatments. However, it is unlikely that the cultivars would have differed in these traits, as they are measured prior canopy closure, thus there is limited opportunity for weed-species related variation between the treatments.

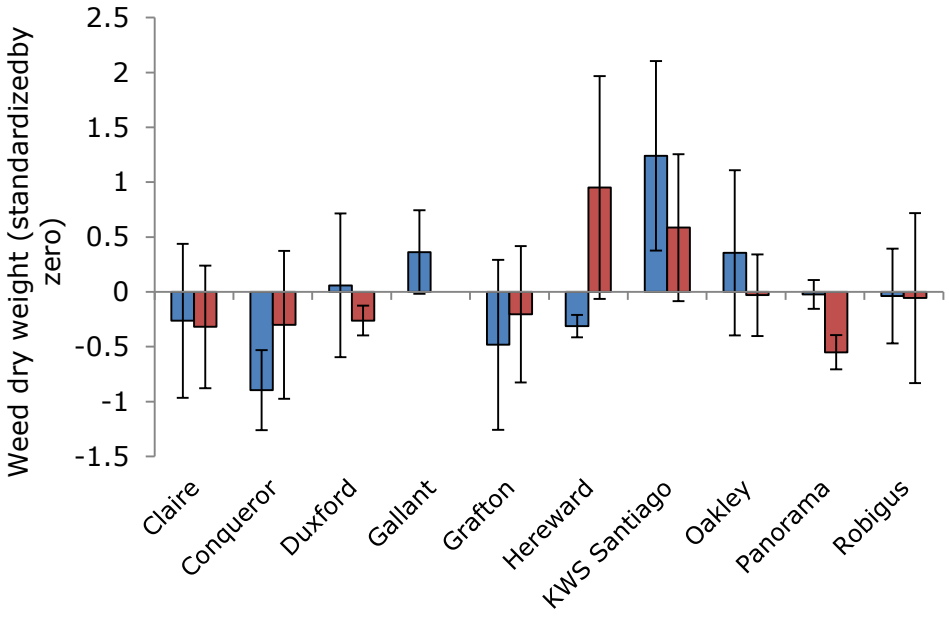

Figure 5.13 - Standardized per plant biomass of *A. myosuroides* and *S. media* when grown in competition with cultivars at different densities, with s.e. bars. All cultivars are wheat. ■ =*A. myosuroides* ■ = *S. media*

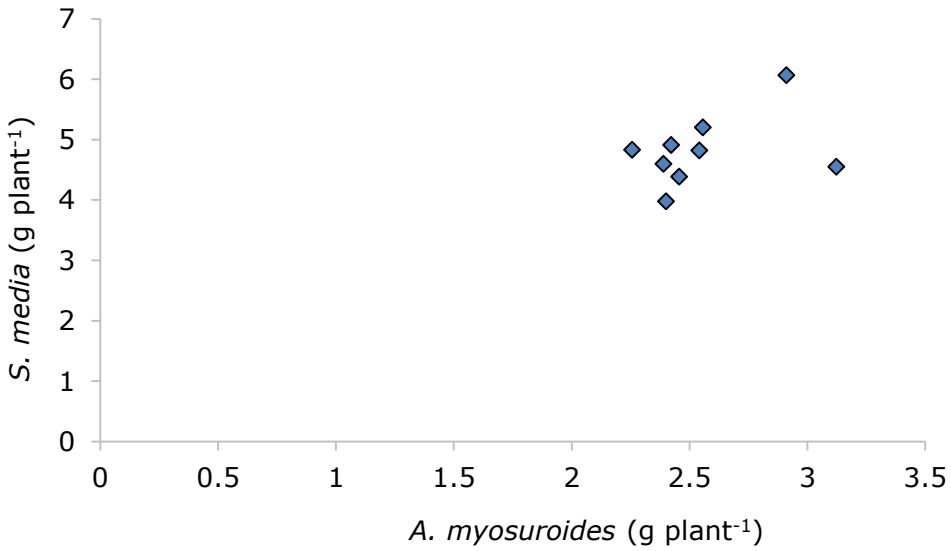

Figure 5.14 - The relationship between the biomass of *A. myosuroides* and *S. media* when grown with different cultivars.

Table 5.7 - Correlation coefficients of wheat traits in relation to *A. myosuroides* and *S. media* biomass. * = P<0.05. *A. myosuroides* n=30; *S. media* n=25.

Cultivar traits	Weed biomass	
	A. myosuroides	*S. media*
TGW	-0.0484	-0.1789
50% emergence	0.1854	0.2032
75% spike emergence	-0.2053	0.048
% stem loss	**0.5239***	n/a
ABGW	-0.1781	0.2861
Early green area	-0.2801	0.017
Early height	0.0172	-0.0595
Early leaf angle	0.1922	-0.0437
Early leaf counts	0.0278	0.1702
Early leaf length	-0.042	0.1506
Early leaf width	0.1755	0.0121
Final height	0.3019	-0.037
Final stem count	-0.3899	n/a
Flag leaf SLA	n/a	0.3456
Flag leaf angle	0.2923	-0.0437
Flag leaf area	-0.1891	**0.455***
Flag leaf length	-0.1296	0.152
Flag leaf width	-0.2023	-0.2773
Highest stem number	0.1014	n/a
LAR	-0.4052	-0.0041
LWR	-0.2302	0.2313
NAR	0.0573	0.1719
RGR_W	0.2114	0.1424
RGR_{GA}	0.1468	-0.2238
Early SLA	-0.083	-0.1879
Rate of tillering	0.2691	n/a
Time of max. growth rate	0.2306	-0.0401
Time of max. stem number	-0.2492	n/a

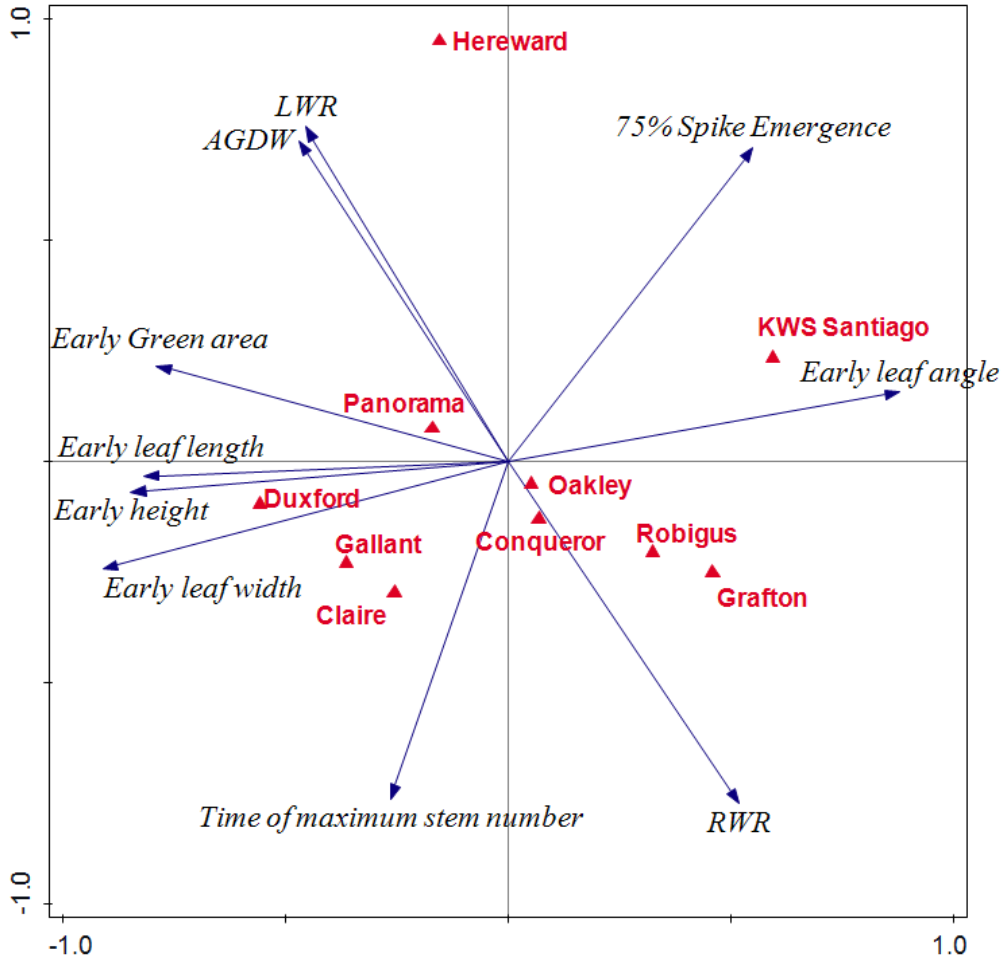

Figure 5.15 - Principal Components Analysis for *A. myosuroides*. Percentage variance accounted for by the two axes = 45.42% (PC1 = 24.95%, PC2 = 20.47%). There was no significant relationship between cultivar scores for PC1 or 2 and *A. myosuroides* dry weight, indicating that neither PC indicated a 'competitive' suite of traits. Only the 10 traits with the highest loadings are shown.

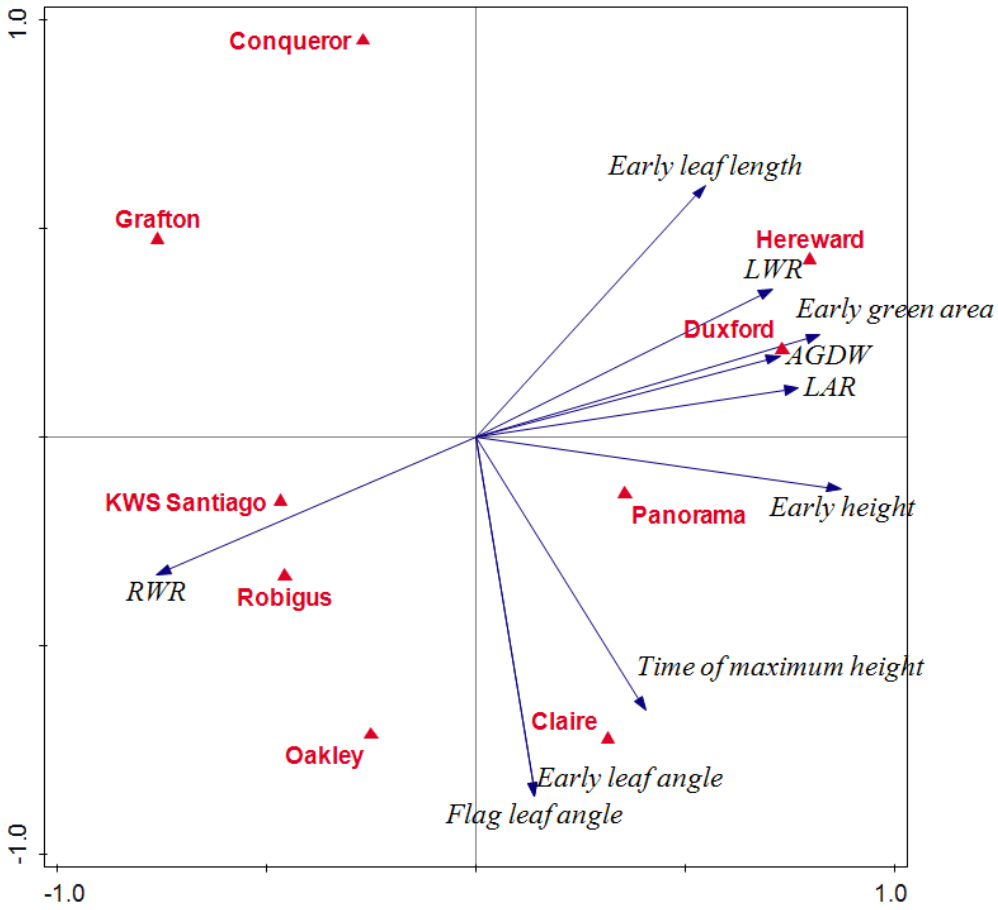

Figure 5.16 - Principal Components Analysis for *S. media*. Percentage variance accounted for by the two axes = 45.51% (PC1 = 26.14%, PC = 19.37%). There was no significant relationship between cultivar scores for PC1 or 2 and *S. media* dry weight, indicating that neither PC indicated a 'competitive' suite of traits. Only the 10 traits with the highest loadings are shown.

5.5 Discussion

5.5.1 Sowing density

In UK arable agriculture, growers will often employ higher seeding rates as part of IWM, owing to its ease, low risk and acceptable costs. Average rates in the UK are now 300-350 seeds m^{-2} (and can exceed 500 seeds $m^{-2)}$ primarily to control *A. myosuroides*. However, with increased crop stand density, yield losses could be expected through increased risk of lodging (Berry *et al.*, 2004), so wheat is rarely sown in excess of these rates.

The increase in crop stand density saw a decrease in *A. myosuroides* seed return – a pattern that has been observed numerous times in the literature (Roberts *et al.*, 2001; Korres & Froud-William, 2002; Auskalniene *et al.*, 2010; Olsen *et al.*, 2012). In a meta-analysis of 19 experiments, Lutman *et al.*, (2013) found that *A. myosuroides* seed head numbers reduced by 15% for every wheat density increase of 100 plants m^{-2} up to the maximum density evaluated (350 plants m^{-2}).

Cultivars differed in their suppressive strength against *A. myosuroides*, a finding that is in agreement with studies of different weed species (Wicks *et al.*, 1986; Mennan & Zandstra, 2005; Ogg & Seefeldt, 1999; Korres & Froud-Williams, 2002). But there was no evidence that the competitive advantage granted by an increased crop stand density differed between cultivars. This suggests that the use of suppressive cultivars and increased stand density are highly compatible strategies. Other studies support the suggestion that competitive ranking will not change with density (Kirkland & Hunter, 1991; Lemerle *et al.*, 1996). However, work by Korres & Froud-Williams (2002) identified three cultivars that did not benefit from an increased sowing density. Though there was no interaction between sowing rate and cultivar, greater replication may have identified cultivars that responded differently to increased density.

One such cultivar could be KWS Santiago, which appears to confer equivalent levels of control under both densities. This may be due to KWS Santiago's relatively prostrate early growth habit resulting in a lower benefit of increasing density (compared to more upright cultivars). This could be due to the prostrate growth habit having limited effect on red:far-red light ratios. In other species, increases in far-red light have been demonstrated to reduce tillering and increase upwards growth

in neighbouring plants, consequently resulting in reduced seed return (Ballaré 1999; Liu *et al.*, 2009). If this mechanism is an important factor in suppressive weed control, then increasing the density of a cultivar such as KWS Santiago would only have a limited effect on red:far-red light ratios. Further work would be required to investigate this hypothesis.

The results suggest that there is an interaction between the traits related to suppressive ability and the crop stand density. This study implies that many of these traits do not have predictive power, with time of spike emergence being the only trait not influenced by stand densities. The other trait, maximum stem number, remains influenced by the density of the crop. The link between early crop spike emergence and reduced *A. myosuroides* seed production suggests a link between the speed of cultivar development and suppressive ability that is consistent across densities, though its importance may reduce at low densities.

Correlation analysis links traits associated with early light interception (greater early green area, early leaf width, LAR and more erect leaves one and two) with enhanced suppressive ability in the high density condition, as discussed in Chapter Three, but fail to contribute to suppressive ability in low density stands. This finding implies that at lower densities, light availability is greater and competition between crop and weed begins later, limiting the importance of these early traits. Higher accumulation of early biomass has been associated with increased PAR interception (Lemerle *et al.*, 1996; Gooding *et al.*, 1993), but little is known about the contribution of traits to suppressive ability across different densities.

Loss of stems was also less important at lower densities, implying that at higher densities, where light competition is stronger, increased stem loss will decrease light interception by the crop (Moeller *et al.*, 2014). However, higher maximum stem number was related to increased *A. myosuroides* seed return, and as such does not follow this trend. This is contrary to expectations, as higher stem number would be expected to increase a cultivar's interception of light. There has been disagreement in the literature regarding the importance of tillering parameters in competition (Lemerle *et al.*, 1996; Huel & Hucl, 1996; Champion *et al.*, 1998). Tillering parameters are complex and highly plastic, and stem number is known to respond to stand density (Champion *et al.*, 1998). It is possible that stem loss is a response to the amount of pressure placed on the cultivar by *A. myosuroides*. This suggests that loss is increased when the weed has been less suppressed earlier in the season, but the limited differences in % stem loss between the two densities provide little support for this notion (see appendices). The correlation between % stem loss and *A. myosuroides* fitness may not be seen at lower densities because both inter- and intraspecific competition was lower. Percentage stem loss was positively correlated to maximum stem number (see appendices), thus higher numbers of stems may be a poor investment of resources when in competition with *A. myosuroides*. Increased maximum stem number has been linked to reduced plant leaf area (Rebetzke & Richards, 1999), so the correlation of this trait may reflect the decrease in leaf area, leading to increased penetration of light from the crop canopy.

Despite the weakening of relationships between suppressive traits at lower densities, the observed relative stability in the

suppressive ranking of cultivars implies that these traits may still be useful in predicting cultivar suppressive ability. Net assimilation rate is the only cultivar trait that is related to *A. myosuroides* seed return at low density, and was not at high density. Net assimilation rate is a measure of net carbon gain and is the physiological component of RGR (Shipley, 2006), but the lack of RGR correlation to suppressive ability implies that it this relationship does not explain the result.

5.5.2 Drilling date

In the UK, mid-September is considered a preferential, and comparatively early, sowing date. In this study it was not possible to drill the crop prior to 4 October, and as such the early drill date is not an ideal representative of the competitive dynamics in an early-drilled crop. The results suggest that the importance of traits differs between the two drilling dates tested, but this difference could be more apparent if the early date had been closer to the September drill dates in agronomic situations.

It is worth noting that when comparing cultivars between different sowing dates, they are not expected to express traits identically. The development of wheat is influenced by photoperiod and temperature – both of which will differ between early and late sowing dates. For this reason, it is important that the experiment be considered in terms of the competitive ability conferred by traits. Associating competitive ability with cultivars.

5.5.2.1 *Suppression*

In agreement with the literature, fewer *A. myosuroides* individuals were present in the late-drill treatment (Lutman *et al.*, 2013), and individuals produced fewer seeds per plant than

the earlier sown date (Melander, 1995). Differences in cultivar suppressive ability are apparent when they are drilled at the end of October, with Claire being the poorest suppressor and Panorama being the strongest. Though there are no discernible differences in cultivar suppressive ability when they were sown at the beginning of October, correlation implies that the ranking of cultivar suppressive ability changes when sow at different dates.

Commercial cultivars in the UK differ in their yield potential when sown early or late, and advice is provided by the suppliers. Although neither principal component could be related to suppression or tolerance, trait loadings did differ between the two sowing dates, suggesting cultivars will develop differently according to environmental factors such as temperature and photoperiod. This could have important implications on both suppressive ability and tolerance of a cultivar. It may be that, when drilled late, suppressive differences are also apparent on the basis that some cultivars require warm temperatures to establish and develop. Few studies have investigated the interaction between drilling date and cultivar choice in suppressive ability, but differences have been noted to be more apparent at earlier drilling dates (Cosser *et al.*, 1997).

An increase in ABGW and traits associated with early green area was related to an increased *A. myosuroides* seed return. When sown later, decreased final stem count was also related to an increase in *A. myosuroides* seed return. It may be that in early drilled crops, early characteristics have a longer period of time over which to influence the growth of *A. myosuroides*, whilst late-drilled cultivars must also rely on competing for resources during stem extension and grain filling. This is supported by the

lack of correlation between seed return and ABGW or early green area traits in the univariate analysis of the late drill treatment. However, another explanation may be that cultivars do not compete as effectively with *A. myosuroides* at later sowing dates. This results in lower final stem counts as the weed dominates access to resources. If this is the case, lower mature stem number is a result of competitive pressure from the weed, rather than a sign of a less suppressive cultivar.

The increased green area leading to reduced suppressive capacity is counter what would be expected, as it should lead to enhanced smothering of the weed (as was seen in the high density treatment on the experiment based on the sand-beds). However, leaf area ratio (LAR) and leaf weight ratio (LWR) were negatively correlated to root weight ratio (RWR) in the ecophysiological traits experiment (see section 2.4.3, Table 2.6). If this relationship is consistent in the field, it could suggest that competition for belowground resources was more important for suppressing weed growth than light competition (as discussed in Chapter Four). The lack of improvement in Claire's performance when sown late may be due to poor investment in belowground structures during the autumn, leaving it in a poor position to compete for soil resources post-winter.

Work on belowground traits and their importance in competition is limited, but studies have shown that competition for belowground resources such as water and nitrogen can be stronger than competition for light (Exlay & Snaydon, 1992; Satorre & Snaydon, 1992; Stone *et al.*, 1998; Wang *et al.*, 2010). As techniques for quantifying root traits develop, the understanding of how root traits contribute to suppressive

ability and tolerance in cereals is expected to improve (Fargione & Tilman, 2006; Stevanato *et al.*, 2011).

5.5.2.2 *Tolerance*

There was no discernible difference in cultivar performance when tested across both drilling dates, but there was an interaction between drilling date and cultivar choice. Cultivar performance was found to differ between the strongest (Panorama) and weakest (Claire) tolerators when the late drilled treatment was examined separately, but no cultivar difference was found in the early drilled plots. This implies that later drilling amplifies the differences in cultivar tolerance to *A. myosuroides*.

No traits provided a consistent relationship to tolerance across both drilling dates. Before reaching a plateau of approximately 500 ears m^{-2}, final stem count is expected to be related to tolerance as greater stem number leads to increased spike number and, consequentially, increased yield of a crop (Mason *et al.*, 2008). However, higher stem counts resulted in greater yield loss in the late drill treatment. This is counter to what would be expected. A possible explanation is that there was a lower proportion of fertile tillers in the late drilled treatment, leading to reduced yield, but without spike counts m^{-2} this cannot be confirmed.

For both suppressive ability and the ability to tolerate *A. myosuroides* pressure, the implication is that trait relationships are not consistent across different drilling dates. However, these conclusions have been drawn from a single year of study. Further understanding of the trait x drilling date interaction could be of value to farmers who wish to use cultivars as part of a weed management strategy. Later drilling date alone

strongly influences *A. myosuroides* seed return, and the contribution of a competitive cultivar is likely to be limited. Tolerance is a more complicated matter, but farmers expect a decrease in yield when sowing wheat later. If delayed drilling reduces *A. myosuroides* establishment to acceptable levels, then cultivar choice is more likely to be based on yield potential when sown at later dates.

5.5.3 Weed species specificity

There was no evidence for differences in the ability of cultivars to suppress the growth of the two weeds, *A. myosuroides* and *S. media*. However, no difference was detected between cultivars when each treatment was examined individually. The experimental year 2012-13 was noted to be the only year out of three where cultivars did not differ in their suppressive ability against *A. myosuroides* in sand-bed based experiments because of the unusually cold winter and spring (Chapter Three). This makes it difficult to draw conclusions from this experiment, and further experimentation would be required to determine if cultivar suppressive ability is weed species-specific.

The problems summarising cultivar suppressive ability across the two weed species persist when seeking to address the central hypothesis of this experiment. The aim had been to determine if traits that enhance suppressive ability against *A. myosuroides* would act similarly to *S. media* - an example of a weed with a contrasting growth habit. Cultivars were observed to be less developed during the winter period of 2012-13 compared to 2011-12 and 2013-14, which may have resulted in increased trait homogeneity across cultivars (as identified in Chapter Three). Increased flag leaf area was related to enhanced *S. media* biomass production, but is difficult to make assertions about this relationship because *S. media* was

harvested prior to flag leaf emergence. However, it has been suggested that larger leaves may benefit shade-tolerant weeds such as *S. media* (Haas and Streibig, 1982)

Increased stem loss was related to increased *A. myosuroides* biomass, but a value for stem loss could not be determined for cultivars grown with *S. media*. This is because the cultivars were relieved of competitive pressure earlier in *S. media* as it was harvested in May, whereas *A. myosuroides* was harvested in July. However, tillering is influenced by plant density, and was shown to differ between cultivars that are growing in a 1:1 ratio with different weed species (Siddiqui *et al.*, 2010). If traits that may be predictors of suppressive ability respond in accordance to the competing weed species and density, it could give false predictions of how suppressive a cultivar may be against a wide range of weed species.

5.6 **Conclusions**

The evidence presented suggests that competitive ranking remains stable between the two stand densities. It was not possible to determine whether the same wheat traits influence suppressive ability at both densities but this is expected to be the case. The importance of early leaf traits and ABGW in high density stands is in agreement with the literature. Inferences are more difficult to draw from the data from the drilling date experiment, where there is no stability in traits related to suppression or tolerance. A more thorough understanding of the relationship between tillering parameters may explain some discrepancies. Evaluation of belowground traits may also explain some unexpected results. The weed-specificity experiment presented limited evidence of trait involvement in the suppression of either *A. myosuroides* or *S. media*. However, it was a problematic experiment conducted in a season that saw

limited trait correlations to weed fitness and no differences in cultivar suppressive ability. As such, the hypothesis cannot be accepted or rejected with confidence, and further experimentation is recommended to gain a greater understanding of the specificity of wheat cultivar suppressive ability.

6 Chapter 6 – Identifying competitive traits and evaluating the contribution of cultivar choice to weed management strategies using the INTERCOM model.

6.1 Introduction

As the previous chapters in this thesis demonstrate, attempts to draw general conclusions about the value of cultivar choice in crop-weed competition are hampered by the complexity of the system. Researchers have tried to capture the processes through modelling. An ideal model would be complex enough to provide accurate predictions and to aid researchers in understanding the processes that drive competition. However, a model should also be readily accessible to use and amend for researchers beyond the development team, whilst being simple enough to be used by non-academics as decision aids in weed management (Weaver, 1996; Wilkerson *et al.*, 2002; Holst *et al.*, 2007).

6.1.1 INTERCOM

Since its initial development, INTERCOM (INTERplant COMpetition) has become one of the most widely used crop-weed competition models. First described and parameterised for sugar beet – *C. album* (Kropff & Spitters 1992; Kropff *et al*. 1992), it has since been adapted for use with multiple crop and weed species. INTERCOM is able to make predictions of crop yield loss based on temperature, the availability of water and soil moisture, and resource assimilation and partitioning by crop and weed. It can also be used to examine different management strategies, such as the density and emergence times of the species.

Though INTERCOM has been parameterized for a wide array of crop-weed species combinations, its use to examine cultivar choice has been limited. The model was found to simulate the competitive outcomes of cowpea (*Vigna unguiculata* L.) cultivars in competition with *Helianthus annus* (L.), but less well with *Portulaca oleracea* (L.) as a weed (Wang *et al.*, 2007). Two rice cultivars were also parameterised by the model, identifying greater leaf area RGR, early height RGR and mature height as important competitive traits (Bastiaans *et al.*, 1997). Early height and green area have been linked to competitive ability in wheat in previous chapters. There are no documented efforts to parameterise the INTERCOM model for different cultivars of wheat in competition with *A. myosuroides*.

This study focused on wheat cultivars in competition with *A. myosuroides*. From the results of the container and field experiments, cultivars have been demonstrated to differ in a number of traits that are used to parameterise INTERCOM. This chapter focuses on *in silico* experiments with the model using empirical data from Chapters Two and Three.

First, sensitivity analysis was used to identify traits that have important implications for predictions of yield loss and *A. myosuroides* fitness. In addition, the model was parameterised for cultivars with different suppressive abilities, and used to predict yield loss and *A. myosuroides* fitness under various environmental conditions. These include varying driver conditions, such as temperature and precipitation, and the impact of increasing crop density and different sowing dates. This provided predictions of the contribution of cultivar choice to integrated weed management strategies under different environmental conditions.

6.2 Aims

In this chapter, the following hypotheses will be tested:

1. Sensitivity analysis will identify wheat traits that have a larger proportional impact on percentage yield loss in weedy scenarios
2. Two cultivars with contrasting suppressive abilities will also have contrasting percentage yield loss predictions from the INTERCOM model, with the cultivar identified as being more suppressive from prior experiments being the more tolerant of the two.
3. Under different climatic conditions and management decisions, the predictions of percentage yield loss for the two cultivars will change.
4. Under different climatic conditions and management decisions, the traits associated with the greatest relative change to percentage yield loss will change and the relative difference between the cultivars will differ.

6.3 Methods

6.3.1 Wheat – *A. myosuroides* INTERCOM model

The INTERCOM-derived model implemented in this study was developed for wheat - *A. myosuroides* interactions by Storkey and Cussans (2007). It was built in C++ and possesses a number of updates to the model described by Kropff and van Laar (1993), such as the inclusion of components of the *Sirius* model (Jamieson *et al.*, 1998) to describe winter wheat growth and partitioning. This integration allowed the model to better account for the growth of wheat in UK arable scenarios specifically including functions for vernalisation and timing of anthesis and grain filling. Other changes to the original INTERCOM model included photothermal time replacing

temperature sum as a mediator of growth and a prompt to switch between distinct developmental stages, and additional calculations for the vertical distribution of leaf area through the canopy. Additionally, a new means of calculating instantaneous assimilation rate using SLA was developed (Storkey & Cussans, 2007) (see section1.7.2.2). Parameters for *A. myosuroides* in competition with wheat were acquired from Storkey (2004; 2005; 2006) using the cultivar Consort, which is no longer on the recommended list.

6.3.2 Sensitivity analysis

Numerous wheat traits are included in the model, and those of interest in this study are listed in Table 6.1. A sensitivity analysis allows the relative importance of each trait to yield loss predictions to be examined. The values used in the original model (Storkey & Cussans, 2007) were the base for the sensitivity analysis and each was reduced in turn by 5%. The model was run, and changes in % yield loss were recorded. These were then compared to a run using the unmodified trait values as a control, to provide a point for comparing % yield loss when individual traits were modified. A sensitivity analysis was conducted for two agronomically-relevant crop densities, (150 plants m^{-2} and 300 plants m^{-2}) and two sowing dates (20 September and 20 October). Emergence times (seven days for *A. myosuroides*, 10 for wheat) and *A. myosuroides* densities (80 plants m^{-2}) were kept constant. The density of *A. myosuroides* was to closely reflect its density in the container experiments (Chapter 3) and the target density in the field. Although the density of *A. myosuroides* from the 2013-14 field experiment could have been used, it was decided that these were low numbers and would not capture the crop-weed competition dynamics as sufficiently. Wheat emergence time was held

constant as it was typically the same in KWS Santiago and Duxford, and ranging from 8 to 11.3 days in the sand-beds experiment between years (see Appendices 6-8).

Table 6.1 - Parameter values for the INTERCOM model. Values for cultivar Consort are those included in the original model and used in the sensitivity analysis. Cultivar values are those used to parameterise for respective cultivar.

Trait	Consort (Storkey & Cussans, 2007)	Duxford	KWS Santiago
RWR	0.71	0.705	0.681
SSA (m^2 g^{-1})	0.003	0.00545	0.00504
Phyllochron (dd $leaf^{-1}$)	90	67.5	69.5
SLA (m^2 g^{-1})	0.019	0.0385	0.0346
RGR_{GA} (cm^{-2} cm^{-2} tt^{-1})	0.0126	0.0116	0.0096
L_0 (cm)	0.64	0.674	0.715
Logistic functions for height			
a (cm)	7.4	1.36	5.73
c (cm)	77.9	81.845	77.299
b (cm ptt^{-1})	0.0085	0.004218	0.005559
m (ptt)	624	685.0	822.6

6.3.3 Parameterising INTERCOM for cultivars

The model was parameterised for wheat cultivars Duxford and KWS Santiago. These cultivars were selected based on the results of the experiments detailed in Chapter Three. In two out of three study years, Duxford was the most suppressive of the cultivars, whilst KWS Santiago was one of the least suppressive.

The experimental work in Chapters Two and Three provided all the data necessary to parameterize the model for each cultivars. The original parameters for wheat and for the two cultivars can be found in Table 6.1. The values were entered into relevant sections of the C++ code, calibrating the model for a single cultivar. The simulation model was run using with temperature and precipitation data recorded at the Rothamsted meteorological station from 2005 – 2014 (harvest year),

acquiring % yield loss values for each year. The model was run with the cultivars at two stand densities (150 and 300 wheat plants m^{-2}) and two sowing dates (20 September and 20 October) that were relevant to weed management strategies.

6.3.3.1 *Phyllochron*

A number of the parameters were not immediately available from experimental data. One of these was phyllochron, which is a measurement of the rate of leaf development (degree days between appearance of a new leaf). The phyllochron is implemented in the model as a trigger for transition from the spring growth phase to the anthesis phase, and is expected to differ between cultivars. The closest equivalent value was for time of 75% spike emergence. The difference between the cultivars time of spike emergence and the succession of leaf generation was calculated (d), giving a DAS measure of when the transition from spring growth to anthesis begins. The phyllochron was changed until the value corresponded with the time of transition. This value was used when modelling the growth and competitive interactions between the cultivar and *A. myosuroides*.

6.3.4 Statistical analysis

For each trait in the sensitivity analysis, yield loss was recorded as a proportional change from the yield loss that was predicted prior to any changes to parameters. The proportional change in yield loss (PCYL) was used as an indicator of the sensitivity of the trait in determining competitive outcomes. A PCYL value for each trait was acquired for every year that the simulation was run.

Model output was evaluated using Genstat 16. The PCYL for each trait was correlated against accumulated thermal time and

total rainfall, to seek evidence that the importance of the trait was related to these environmental conditions. A simple linear regression with groups was used to examine the difference between the two cultivars responses to accumulated thermal time.

Differences between cultivar predicted yield loss were tested using a factorial ANOVA, allowing for interactions between cultivar, crop density and crop sowing date to be evaluated. As yield loss was expressed as a percentage, it underwent a logit transformation. The data followed a normal distribution.

6.3.4.1 *Use of the rectangular hyperbola to study impact of increasing crop density*

The INTERCOM model includes density and sowing date of the crop, which permits predictions based on the use of both as weed management strategies. It anticipates the relationship between percentage yield loss and two commonly-employed weed management strategies, crop density and crop sowing date, to follow a rectangular hyperbola (equation 1).

$$Y = a + \frac{b}{(1 + D + x)} \qquad (1)$$

The rectangular hyperbola was used to derive a value for comparison between the use of a cultivar and sowing time or crop density as a means to resist yield loss. The rectangular hyperbola was applied to output from the model, and the % yield loss of Duxford at low values of crop density compared to values of crop density for equivalent % yield loss for KWS Santiago. This process was also conducted for the % yield loss / sowing time rectangular hyperbola. The process provides values of comparison as predicted by INTERCOM, allowing for the benefit of a stronger performer to be understood in terms

of the benefits acquired by delaying sowing and increased crop density.

6.4 **Results**

6.4.1 Yield loss and *A. myosuroides* biomass

The model outputs both % yield loss of wheat and *A. myosuroides* biomass. The model treats both as closely correlated (r = 0.86; P<0.001), as increased *A. myosuroides* will result in increased competition with the crop, resulting in elevated yield loss (Figure 6.1). Biomass and seed return of *A. myosuroides* are closely correlated (see Chapter Three). As such, the examination of % yield loss can be considered a proxy for suppressive ability.

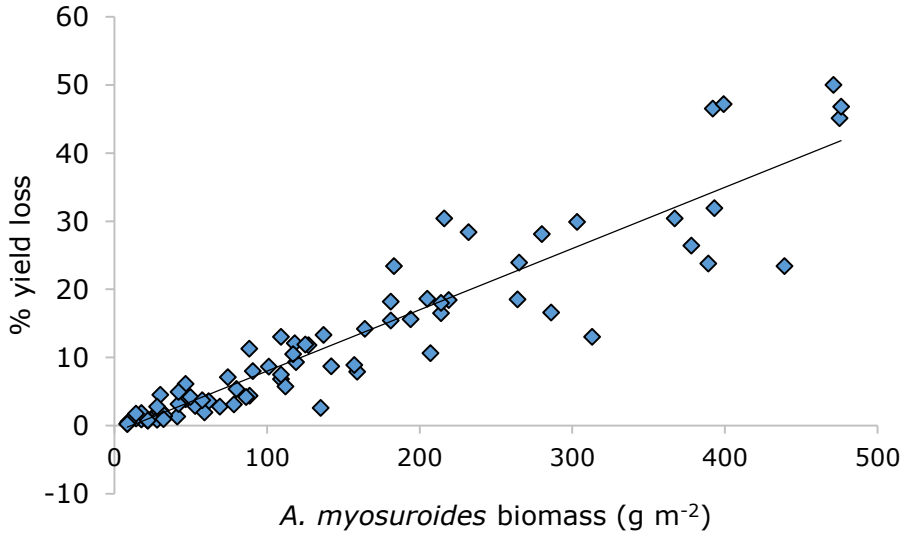

Figure 6.1 - The relationship between INTERCOM predictions of wheat yield loss and *A. myosuroides* biomass. Data points are derived from model runs for Duxford and KWS Santiago under four scenarios.

6.4.2 Weather

Accumulated thermal time was an important determinant of yield loss predictions in the INTERCOM model for both cultivars ($F_{1,76}$=21.62, P<0.001), with KWS Santiago having a marginally steeper slope than Duxford ($F_{1,76}$=3.87, P=0.053), and higher

% yield loss always observed for KWS Santiago ($F_{1,76}$=34.33, P<0.001). In the coldest year, 2013, the model reported the lowest yield loss prediction of 3.21%, whilst the second highest was in the warmest year (2006 with 17% yield loss) (Figure 6.2). In the coldest year, *A. myosuroides* biomass was lowest, whilst the warmest year was that with the highest *A. myosuroides* biomass (Figure 6.3). The predicted weed-free yield of wheat suffered no equivalent detriment in the colder years (Figure 6.4), implying that temperature has a stronger impact on *A. myosuroides* competitive performance than on wheat.

Yield loss values did not differ to the same degree between the driest and wettest year (2011 and 2014, respectively) (Figure 6.5). No correlations were seen between % yield loss and total rainfall. The UK's temperate maritime climate, where extended periods without rainfall are infrequent, may explain why no impact of precipitation was evident from the dataset.

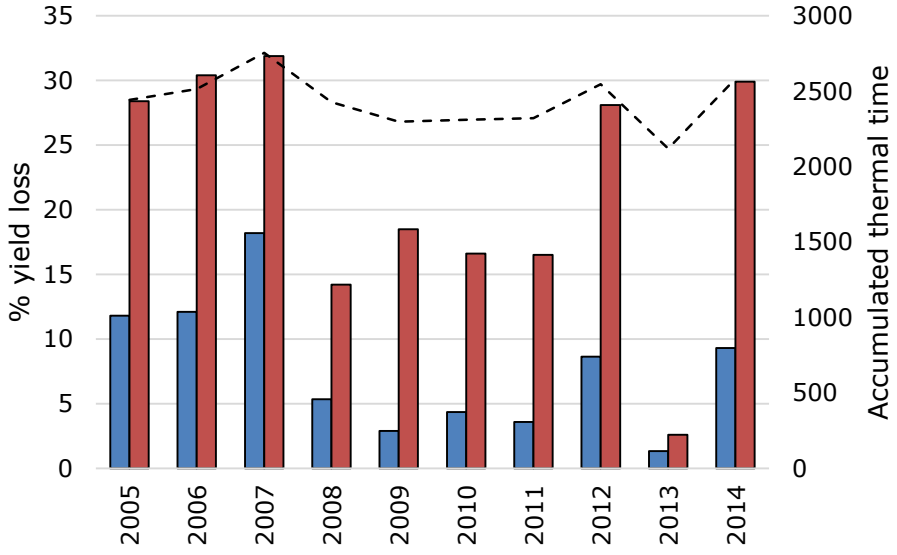

Figure 6.2 - INTERCOM predictions of % yield loss from years 2005-2014, and the accumulated thermal time of each year (dashed line). ■ = Duxford; ■ = KWS Santiago. Crop density 300 plants m^{-2}, sown 20th September, *A. myosuroides* density 80 plants m^{-2}.

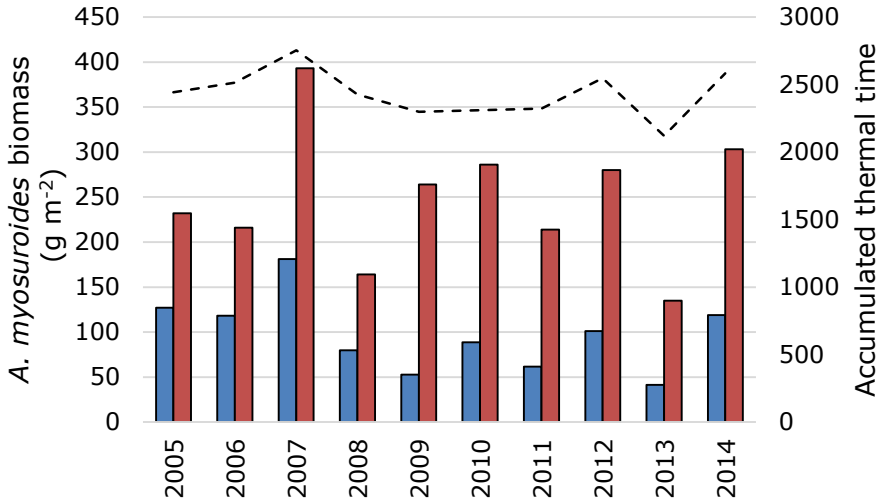

Figure 6.3 - INTERCOM predictions of *A. myosuroides* biomass in competition with wheat cultivars from 2005-2014, with accumulated thermal time of each year (dashed line). ■ = KWS Santiago. Crop density 300 plants m^{-2}, sown 20 September, *A. myosuroides* density 80 plants m^{-2}.

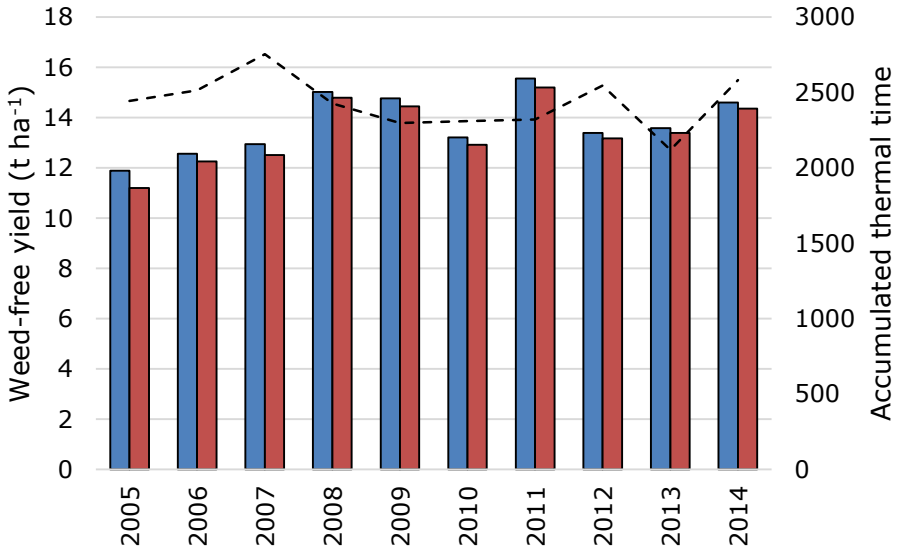

Figure 6.4 - INTERCOM predictions of weed-free yield of wheat cultivars from 2005-2014, and the accumulated thermal time of each year (dashed line). ■ = KWS Santiago. Crop density 300 plants m^{-2}, sown 20 September, *A. myosuroides* density 80 plants m^{-2}.

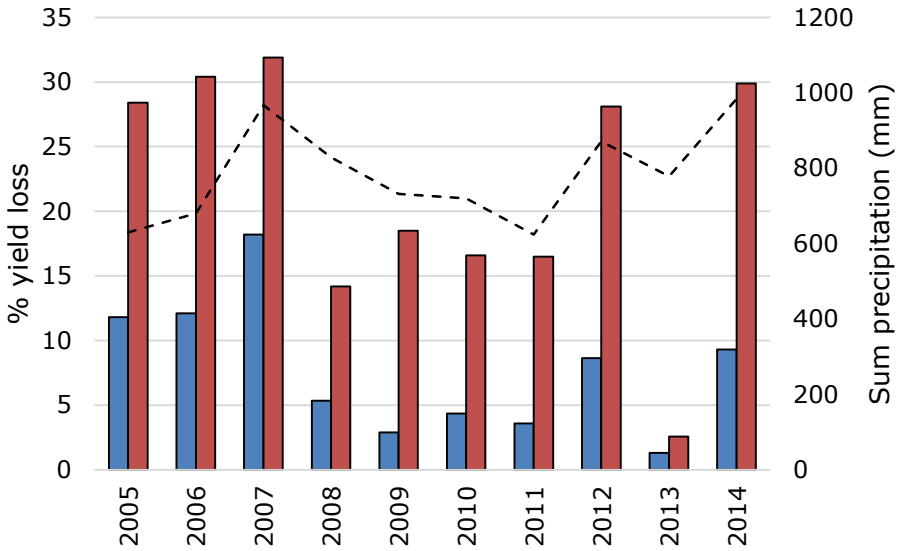

Figure 6.5 - INTERCOM predictions of *A. myosuroides* biomass, from 2005-2014, and the sum precipitation for each year (dashed lined). ■ = Duxford; ■ = KWS Santiago. Crop density 300 plants m^{-2}, sown 20 September, *A. myosuroides* density 80 plants m^{-2}.

6.4.3 Sensitivity analysis

There was a difference in how traits influenced the proportional change in yield loss of the crop. Figure 6.6 demonstrates the impact of a 5% decrease in the original trait values on the proportional change in yield loss compared to a simulation run on the original values. Negative numbers indicate a decrease in yield loss when the trait is decreased by 5%.

The INTERCOM model predicts that an earlier time of mature height (parameter *m*) is synonymous with decreased yield loss (and, by proxy, decreased *A. myosuroides* biomass). But it also predicts a lower rate of leaf production by the wheat results in decreased yield loss. This is unlikely, as rapid maturity is paired with increased leaf prediction. The model currently treats them as independent parameters and it is likely that this unexpected result is an artefact of the model structure.

The PCYL for each trait was not correlated to sum precipitation in any of the four scenarios, and was infrequently correlated to

accumulated thermal time. Only the traits associated with the logistic function of heights were correlated, and to varying degrees across the four management scenarios (Table 6.2).

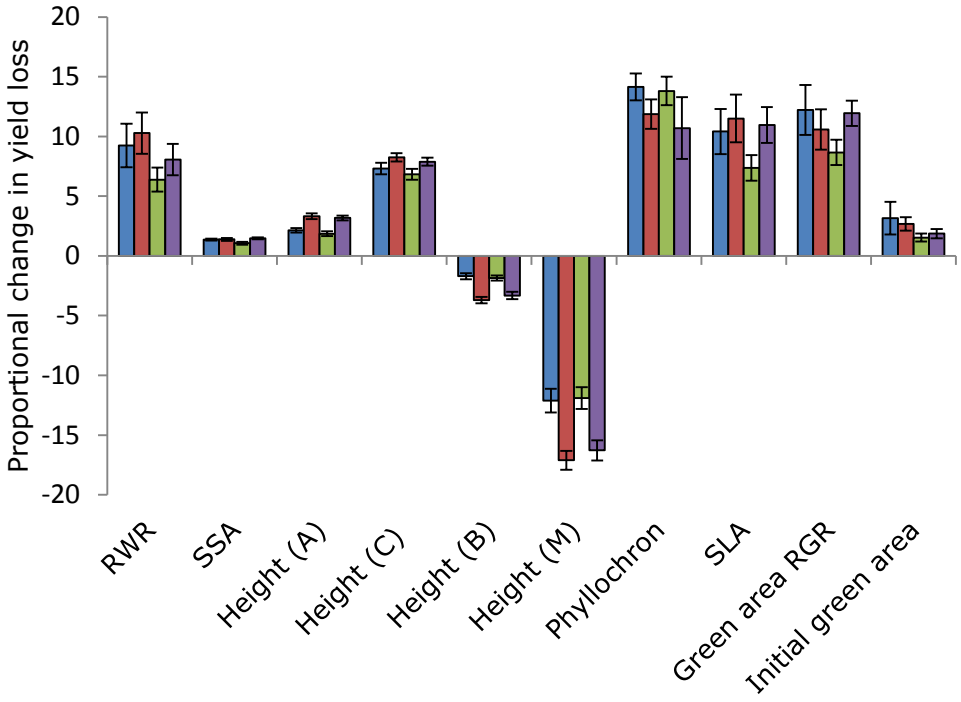

Figure 6.6 - The mean proportional change in % yield loss when INTERCOM parameter traits are decreased in value by 5%. Simulation model was run with weather data from 2005-2014. ■ = 300 plants m^{-2} sown 20 Sept; ■ = 300 plants m^{-2} sown 20 Oct; ■ = 150 plants m^{-2} sown 20 Sept; ■ = 150 plants m^{-2} sown 20 Oct. Bars indicate standard error.

Table 6.2 - Correlation coefficients of PCYL for height logistic functions to accumulated thermal time. * = P<0.05; ** = P<0.01; *** = P<0.001.

	150 x 20	150 x 50	300 x 20	300 x 50
a	-0.4838	-0.6029	-0.6107	**-0.6639***
b	0.5928	0.418	**0.6353***	0.4349
c	**-0.7784****	-0.5235	**-0.8816*****	-0.6117
m	**0.656***	0.4021	**0.7065***	0.4783

6.4.4 Cultivar competitive ability

The cultivars Duxford and KWS Santiago represented the strongest and weakest suppressors of *A. myosuroides*, respectively, in the study detailed in Chapter Three. By parameterising the model for these two cultivars, we see that

the cultivars maintain the same suppressive ranking (Figures 6.7 and 6.8), also contrast in their % yield loss when under pressure from *A. myosuroides in silico* (Figures 6.9 and 6.10).

In each weed management scenario, Duxford maintained a lower *A. myosuroides* biomass and % yield loss than KWS Santiago ($P<0.001$; 1 d.f.). They were also determined by crop density ($P = 0.01$; 1 d.f.) and sowing date ($P<0.001$; 1 d.f.), demonstrating the importance of these management strategies in the model. There was no significant interaction between these strategies. The differences between the two cultivars were more extreme at a 150 plants m^{-2} density / 20 September sow date.

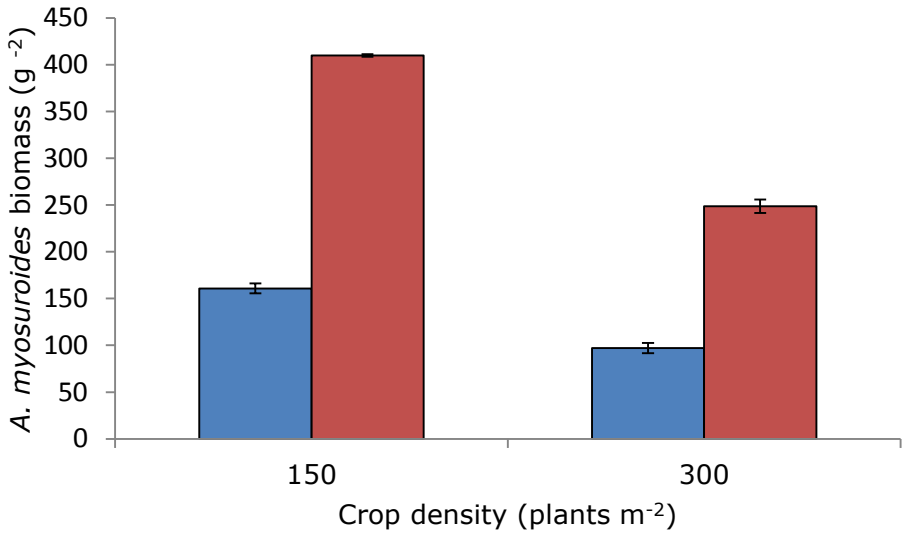

Figure 6.7 - The INTERCOM predictions of *A. myosuroides* seed return when grown with cultivars Duxford and KWS Santiago at different crop densities. The model was run using weather data from 2005-2014. Sowing date 20 September. ■ = Duxford; ■ = KWS Santiago

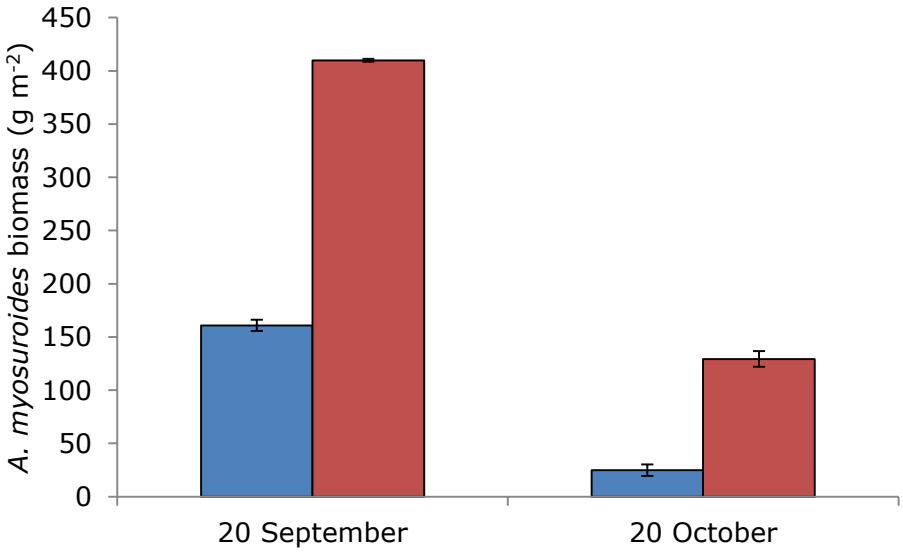

Figure 6.8 - The INTERCOM predictions of *A. myosuroides* seed return when grown with cultivars Duxford and KWS Santiago at different sowing dates. The model was run using weather data from 2005-2014. Crop density 150 plants m^2. ■ = Duxford; ■ = KWS Santiago

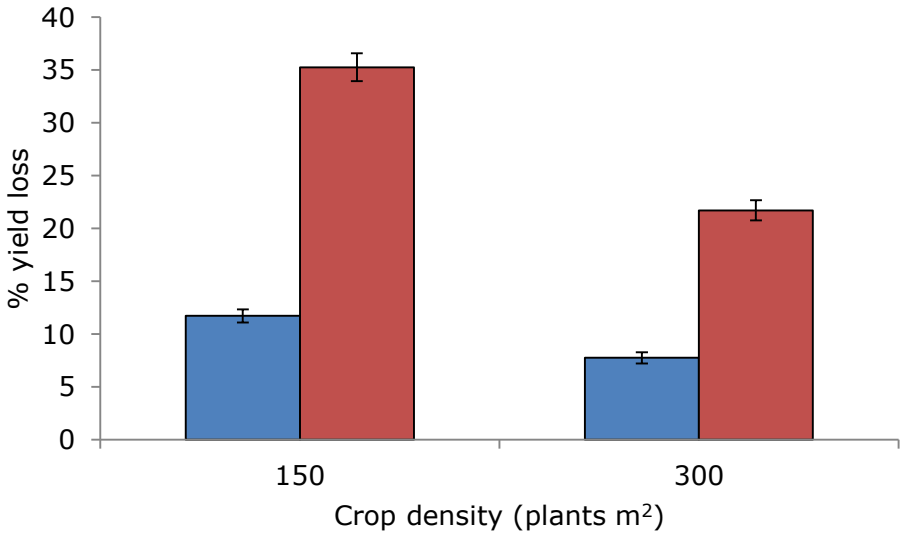

Figure 6.9 - The INTERCOM predictions of % yield loss for cultivars Duxford and KWS Santiago sown at different densities. The model was run using weather data from 2005-2014. Sowing date 20 September. ■ = Duxford; ■ = KWS Santiago

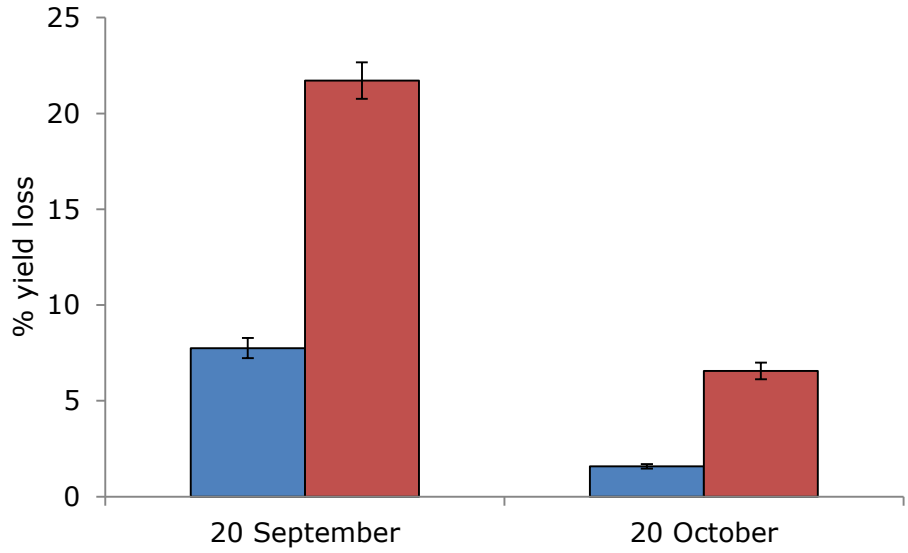

Figure 6.10 - The INTERCOM predictions of % yield loss for cultivars Duxford and KWS Santiago sown at different dates. The model was run using weather data from 2005-2014. Sowing density 150 plants m^2. ■ = Duxford; ■ = KWS Santiago

6.4.5 The contribution of cultivar choice to IWM

A reduction in yield loss was observed with increasing crop stand density, and eventually begins to reach the point of diminishing returns. The model anticipates Duxford to outperform KWS Santiago at all densities, though the differences between cultivars are higher than would be anticipated when compared to those observed in the container and field experiments (Chapters Three and Four). This is worth considering when observing the rest of the model outputs.

In order for KWS Santiago to achieve a similar yield loss to Duxford sown at 150 plants m^{-2} (mean % yield loss of 11.7), its stand density must be increased to 640 plants m^{-2} (Figure 6.11). The impact of sowing date has a similar effect, with Duxford consistently more competitive than KWS Santiago (Figure 6.12). A rule of diminishing returns also follows here, with the greatest difference in weed-related yield loss between neighbouring dates observed between earlier dates. In order for KWS Santiago to achieve a similar yield loss to Duxford sown at

150 plants m^{-2} and on 20 September (mean % yield loss of 11.7), its sowing must be 16 October.

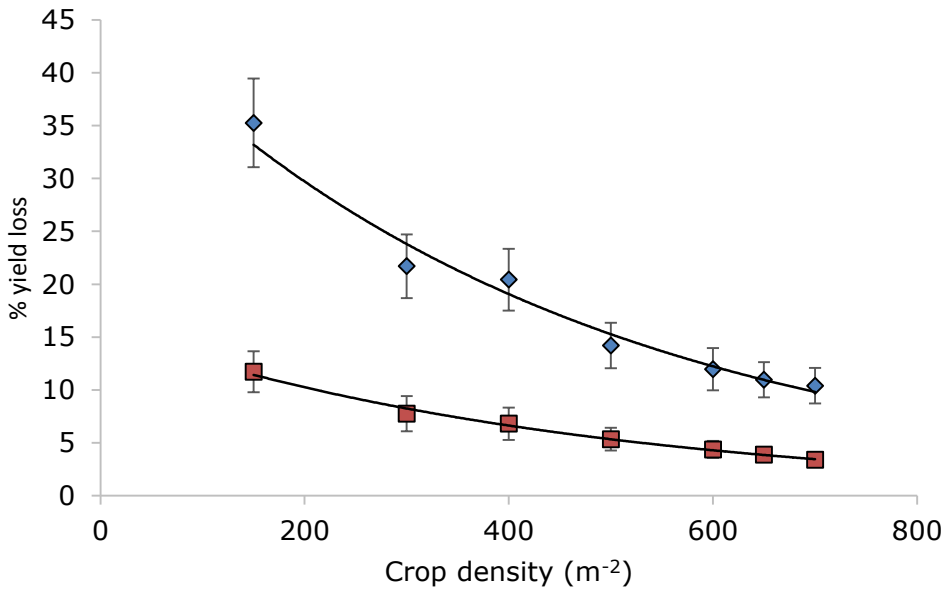

Figure 6.11 - The % yield loss predictions of cultivars when sown at different densities, with *A. myosuroides* at 80 plants m^{-2}. Sowing date 20 September. Bars denoted standard error. ◆ = KWS Santiago ■ = Duxford

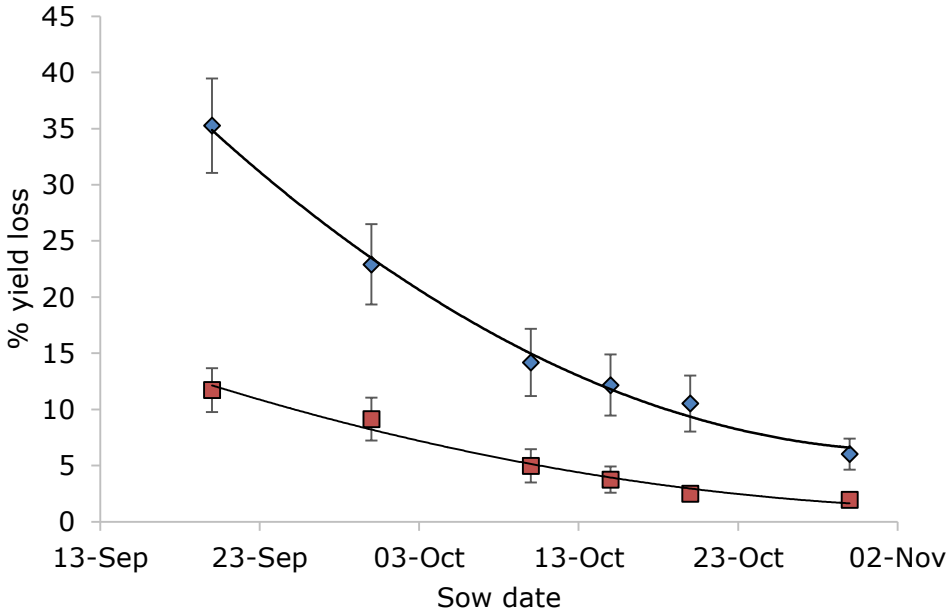

Figure 6.12 - The % yield loss predictions of cultivars when sown at different dates. Crop density 150 plants m^{-2}, *A. myosuroides* density 80 plants m^{-2}. Bars indicate standard error. ◆ = KWS Santiago ■ = Duxford

6.5 Discussion

6.5.1 Traits related to competitive ability

Many traits have been related to competitive ability in the literature and in this thesis. Of those represented in the INTERCOM model, many change in the manner anticipated. These include the increase in yield loss as mature height, RWR, SLA and RGR_{GA} are decreased. Kropff *et al.*, (1992) reported leaf area RGR and SLA to effect the predictions of yield loss substantially in a model parameterised for sugar beet, whilst Bastiaans *et al.*, (1997) found leaf area RGR, early height growth rate and maximum height to be the most important determinant in a model parameterised for rice. This demonstrates that these provide a strong synopsis of the relationships between traits and competitive ability. However, the relative importance of similar traits in sensitivity analyses conducted across these different species may be an artefact of the model. As such, they must be treated with caution. For example, the outcome of the present sensitivity test is similar to the one performed by Kropff *et al.* (1992) testing interspecific competition between sugar beet and *C. album*.

Precipitation had no influence on the sensitivity of traits. Thermal time only influenced the sensitivity of parameters derived from the logistic function of height, though not across all management scenarios. As the logistic function is driven by thermal time the correlation is expected, but its influence on competitive dynamics is dependent on the time of sowing and stand density. However, the sensitivity of these traits was still consistent across different management scenarios. Given the much decreased *A. myosuroides* biomass in the coldest year compared to warmer years, and the limited impact that temperature had on wheat yield, it is assumed that warmer

autumn and springs will result in increased competitive ability in *A. myosuroides*. This is in accordance with recent studies on the impact of environment on weed competition that demonstrated increased yield loss from weeds (with *A. myosuroides* being a major component) on the Broadbalk long term experiment in warmer years (de Leon *et al.*, 2014).

Some of the traits of greatest sensitivity in the model have been related to competitive ability *in situ*. Mature height has long been associated with wheat in competition with a variety of weed species (Challaiah *et al.,* 1986; Christensen, 1995; Ogg & Seefeldt, 1999; Vandeleur & Gill, 2004). Traits associated with early vigour, of which RGR_{GA} is a component, have been linked to increased suppressive ability (Huel and Hucl, 1996; Coleman *et al.,* 2001), and the value of root competition has been demonstrated in studies (Satorre & Snaydon, 1992). Decreased specific leaf area has been associated with low competitive ability (Olesen *et al.,* 2004), as it is linked to a life history strategy which is less flexible to changes in the canopy to better compete for light.

However, the structure of the model predicts some trait changes to have an impact on competitive outcomes than would not be expected *in situ*. The most evident example is the relationship of proportional change of yield loss to both phyllochron and *m* (the time at which mature height was attained). These two traits are closely related, with leaves being produced as the crop grows upright, and terminating at a similar time. It is highly unlikely that a crop can slow leaf production and increase height growth simultaneously. This is observed in the sensitivity analysis because the model treats these traits as though they are wholly independent, but genetic links would be expected. Bastiaans *et al.*, (1997) had similar concerns when

applying the INTERCOM model to rice cultivars, particularly regarding maximum height and yield potential. Additionally, the phyllochron was determined indirectly in this study, and the resulting value for each cultivar differed greatly from that of the cultivar which the model was originally parameterised for. Any interpretation of the importance of the phyllochron based on this study must be done with extreme caution.

The INTERCOM model focuses on competition for light and soil moisture, the acquisition of which is mediated by parameters of growth and temperature. Of the two resources, light is modelled in greatest detail, focusing on interception by the canopy, and the rate of assimilation. By comparison, soil moisture is partitioned between the competing species depending on their RWR, and the model considers if the volume acquired by each species is enough to fill requirements for growth. The fine detail of belowground competitive interaction is not considered in the version of the model used in this analysis, and its inclusion is limited by the difficulty in quantifying the importance of belowground traits in competing for water. Model algorithms have been developed that divide the soil into layers and predict resource competition as a function of root distribution. We did not have sufficient data on below ground traits to explore these processes in detail but there is evidence from a study on the impact of climate change on *A. myosuroides* competition that late season drought can play and important part in determining the outcome of competition (Stratonovitch *et al.*, 2012). The value of including more detail on belowground interactions is uncertain. It could be argued that, in the UK, using a model that focuses on light competition is justified, as the temperate maritime climate means that a drought-scenario is observed less frequently. However, post-anthesis droughts are commonly

observed, and climate change may increase water scarcity. Representation of competition for belowground resources are likely to improve as the understanding of the traits involved improves.

The model also assumes that other belowground resources are in ample supply. Authors such as Bastiaans *et al.*, (1997) have voiced concern that this may not be reflected *in situ* (Bastiaans *et al.*, 1997). There are also concerns that phonological plasticity is not captured sufficiently in models (Cavero *et al.*, 2000; Weaver 1996). However, these facets, and their influence on competition, are difficult to capture in a model, and elevated complexity may not necessarily improve predictive accuracy (Deen *et al.*, 2003) and would further reduce their accessibility (Wilkerson *et al.*, 2002). The results reported within imply that the current model is adequate for identifying competitive traits, but further validation would be needed to confirm this, particularly in different localities.

6.5.2 Competitive cultivars and weed management

The model predicted that Duxford and KWS Santiago would differ in their ability to compete against *A. myosuroides*. The findings agreed with those in Chapter Three, where Duxford was a stronger competitor than KWS Santiago. This could be attributed to a number of traits that were identified by the sensitivity analysis. Duxford possessed greater SLA, RGR_{GA}, RWR and reached mature height before KWS Santiago, which would have contributed to Duxford's better performance in the model. As such, INTERCOM can be deemed satisfactory in identifying competitive cultivars based on traits. The projected improvement in weed tolerance and seedbank management from the two study cultivars is larger than anticipated and needs to be verified through field studies.

The differences between the cultivars was also maintained when sown at higher densities and later sowing dates. This implies that the ability of cultivars to compete against *A. myosuroides* is fully compatible with both of these weed management strategies. Such a finding would be welcome by those seeking additional means to control *A. myosuroides*.

The simulation model predicted that, in order for KWS Santiago to reduce yield loss to the same extent as Duxford at 150 plants m^{-2}, it must be sown at over four times that density. However, 600 plants m^{-2} is an unrealistic target for producers due to factors related to space limitations and the cost of the additional seed. An increase to crop density operates under the principle of diminishing returns, which is accounted for by the model. For density, this is owing to the fact that each additional wheat plant added to the stand will increase crop canopy dominance by a smaller quantity and interspecific competition becomes more important (Cousens, 1985b). In addition, there is an increased risk of lodging at high densities, leading to yield reductions for which the model cannot account. As such, there is a careful balance for growers wishing to maximise the crop's advantage over the weed.

In order for KWS Santiago to match Duxford's lower % yield loss when sown on 20 September, an approximate sowing date of 16 October is advised by the model. However, delaying sowing date has a behaviour that is similar to increased sowing density. The INTERCOM model treats the impact for sowing date as decreasing *A. myosuroides* competition as a rectangular hyperbola, reflecting the decreased germination of *A. myosuroides* at colder temperatures. Delaying sowing aims to reduce *A. myosuroides* numbers by missing its primary germination window, which is September and early October

(Colbach *et al.*, 2007). But delayed sowing has associated risks not captured by INTERCOM, such as poor crop establishment or poor weather in late autumn preventing the farmer from sowing the crop at all. Although maximal benefit is achieved by delaying until early November, few growers are willing to risk such a late target drill date (Lutman *et al.*, 2013).

The model predictions must be treated with caution, as they do not accurately reflect experimental findings. Although Duxford was regularly a stronger suppressor than KWS Santiago, the difference between the pair appears to be exaggerated by the model. This is likely due to facets that the model does not capture. One of these is belowground competition, which could be a stronger determinant of competitive outcomes. In addition, there are aboveground traits that experiments related to suppressive ability but are not adequately captured by INTERCOM. These include facets of stem productions and loss, which have been explored in previous chapters and appear to have complex interactions with competitive outcomes. The importance of both belowground traits and stems would need to be better understood before their possible addition to a model could be considered.

6.5.3 Conclusions

In summary, the INTERCOM model for wheat – *A. myosuroides* simulates the impact of wheat traits on final competitive outcomes as would be expected from the literature. The model was parameterised for two cultivars of wheat with contrasting competitive abilities and ranked them as would be anticipated. The model suggests that cultivar choice is a viable, low-risk alternative in weed management. Sowing a cultivar more similar to Duxford than to KWS Santiago would provide enhanced *A. myosuroides* suppression and yield retention

without the risks inherent to sowing date and crop density. However, *in situ* validation of the model, particularly of the purported equivalency of cultivar choice to crop density or sowing date, would be of value (Deen *et al.*, 2002).

7 General Discussion and Conclusions

7.1 Introduction

As the ability to control weeds through the use of herbicides diminishes, farmers have begun incorporating different approaches for managing problematic weeds into IWM. Competitive cultivars have potential as an inexpensive weed management tool. The search for cultivars that possess strong competitive ability, expressed either as suppression of weed populations or tolerance of weed pressure, has been a long-term endeavour in various crops (Appleby *et al.*, 1973; Huel & Hucl, 1996; Zhao *et al.*, 2006; Auskalniene *et al.*, 2010). Identifying competitive cultivars requires a trait-based approach, as traits may be used to rank cultivar competitive ability and breed new cultivars (Coleman *et al.*, 2001; Hansen *et al.*, 2008).

The three central questions of this thesis were:

1. Can competitive traits be identified in wheat?
2. Can these traits be used to screen cultivars for tolerance and suppressive ability?
3. How does cultivar choice contribute to commonly employed weed management strategies?

7.2 Suppressive traits in wheat

Of the wheat cultivars in this study only Duxford and KWS Santiago were consistently good and poor suppressors, respectively. These cultivars differed markedly from one another, with Duxford being taller at earlier growth stage, with a greater green area, erect leaves and fewer tillers. KWS Santiago had lower green area and a short, planophile growth form during winter months and produced more tillers. These traits were useful for explaining variance in suppressive ability

and these two cultivars illustrate the combined impact of low- or high-suppressive traits on competitive outcomes.

The remainder of the cultivars did not have a consistent rank when compared across experiments, and differences between cultivars expressed in containers were often not observed in the field. The cultivars in these studies were all UK semi-dwarfs (except Maris Widgeon, included in 2011-12 only) and from a narrow genetic background. Cousens and Mohktari (1998) reported a similar trend in a selection of Australian cultivars. Breeding for higher yield potential in near-ideal conditions may have restricted traits that are important in non-ideal conditions, such as when growing under competitive pressure from weeds. This means the cultivars do not differ greatly in their suppressive ability, leaving traits harder to identify than in studies where a wide range of cultivars are tested (Lemerle *et al.*, 1996). This may explain why few traits consistently emerged as suppressive and none as tolerance traits (Table 7.1). Increasingly, research efforts are exploring the genetic heritage of wheat (for example, Cuniff *et al.*, 2014), and its incorporation into commercial cultivars may see important traits represented along a wider gradient.

Frequently, suppressive ability and tolerance were positively-related. If the conclusions drawn by Wang *et al.*, (2010) regarding tolerance are correct, cultivars that are successful suppressors would be considered good tolerators by proxy, as the suppressive cultivars have been better able to acquire resources, limiting *A. myosuroides* growth and its ability to compete with wheat as the season progresses. There is some appeal in this idea, as early aboveground weight was associated with suppressive ability and enhanced tolerance of *A.*

myosuroides. However, no trait was related to tolerance and suppression in the same experimental year.

7.2.1 Early vigour

Traits expressed prior to canopy closure (early green area, early aboveground weight and early height) frequently emerged as a key variables explaining differences between cultivars in the suppression of *A. myosuroides* (Table 7.1). The importance of these early growth traits, which have been used as indicators of early vigour, has been highlighted in other studies (Weavers *et al.*, 1994; Ogg and Seedfeldt, 1999; Olesen *et al.*, 2004). This indicates the importance of pre-emptive resource acquisition in competitive success in the context of asymmetric resource competition.

In the experiments, an attempt was made to identify the role of specific components of early vigour in determining the outcome of competition including initial size and RGR during the exponential growth phase. Seedling RGR_{GA} and initial green area were captured in the RWGA and INTERCOM models as a means to ascertain dominance of the canopy by both weed and cultivar. Neither correlated with *A. myosuroides* seed return in the container-based experiments, and could not be adequately quantified in the field. However, the models used these values to determine each species' share of the canopy upon its closure. As RGR_{GA} and L_0 (initial green area) would determine the early green area of a cultivar – a trait that was associated with suppressive ability – its value can be considered justified as successfully summarising important components of competitive ability.

Greater early green area and early height may influence competitive outcomes before canopy closure because of

processes other than resource competition. As greater green area surrounds a plant, a higher proportion of far-red to red light is reflected onto it. Such changes in red:far-red light ratios can induce a change in plant growth form, prompting increased upright growth at the expense of tiller production (Ballare, 1999; Liu *et al.*, 2009). If *A. myosuroides* responds in a similar manner, it would explain the lower seed return, as fewer fertile tillers would be produced. Early height may contribute to this due to the low angle of the sun during the winter months allowing increased far-red light to be reflected. This hypothesis would merit further investigation.

Table 7.1a. Pearson's correlation coefficients for traits versus *A. myosuroides* seed return across all experiments. Only traits reported as significant in at least one experiment were included.

	Sandbeds				In-field		
Cultivar traits	2011-12	2012-13	2013-14 High density	2013-14 Low density	2012-13	2013-14 Early drill	2013-14 Late drill
% stem loss	n.a	0.3236	**0.4906****	0.036	0.214	-0.0635	0.3838
Early aboveground weight	**-0.3722***	-0.2274	-0.2269	-0.2269	-0.1957	**0.5466****	-0.1155
Early green area	**-0.4472****	-0.3571	**-0.5024****	0.0863	-0.1496	**0.4708****	0.0682
Early height	**-0.5362*****	-0.1038	**-0.3793***	-0.1039	-0.2876	0.2143	-0.2009
Early leaf angle	n.a	0.4072	**0.522****	-0.0449	n.a.	n.a.	n.a.
Early leaf number	-0.0276	0.2092	0.1905	-0.1634	0.2197	**0.4968****	-0.1865
Early leaf width	n.a.	0.1578	**-0.4129***	0.0261	0.1408	0.0543	n.a.
Final stem count	n.a	-0.2404	-0.3492	-0.0999	-0.1037	0.2959	**-0.6165****
Flag leaf length	**-0.3997***	-0.1554	0.1278	0.2463	-0.2369	0.063	-0.3319
Leaf area ratio	**-03555***	**-0.4804***	**-0.5228****	-0.1517	n.a.	n.a.	n.a.

Table 7.1b. Pearson's correlation coefficients for traits versus *A. myosuroides* seed return across all experiments. Only traits reported as significant in at least one experiment were included.

	Sandbeds				In-field		
Cultivar traits	2011-12	2012-13	2013-14 High density	2013-14 Low density	2012-13	2013-14 Early drill	2013-14 Late drill
Maximum stem number	**0.3301***	0.096	**-0.5573****	-0.1015	0.1359	0.2181	0.0803
Net assimilation rate	-0.1469	0.0275	0.1919	**0.395***	n.a.	n.a	n.a
Specific leaf area	**-0.4518***	-0.141	-0.3693	-0.007	0.1172	0.0945	0.1721
Thousand grain weight	-0.0082	-0.0611	**0.5706***	0.3037	-0.0781	-0.0949	-0.1459
Time of % spike emergence	n.a.	-0.1012	**0.4419***	0.2049	n.a	n.a	n.a

7.2.2 Development traits

Traits associated with later stages of development were also related to *A. myosuroides* seed return. Faster spike emergence and lower maximum tiller number increased suppressive ability in a number of experiments, suggesting that rapid development and conserved tillering are part of a suppressive strategy. Rapid development would reduce height differential between wheat and *A. myosuroides* during the spring and lead to greater resource acquisition during late-season competition. Conserved tillering would see less resources wasted due to reduce tiller dieback (supported by evidence of reduced % stem loss also being linked to increased suppressive ability). In summary, a competitive cultivar would be that which not only develops quickly, but invests resources appropriately for further resource acquisition.

The apparent competitive ability conferred by fewer tillers may be because resources are allocated to another process that is of greater competitive value, possibly one not examined in this thesis such as belowground structures. If this is the case, it would imply that late-season competition is for the belowground resources of soil moisture and nutrients, not for light. A study of the potential impact of climate change on competition from *A. myosuroides* has indicated that belowground competition is an important driver of the system supported the argument that belowground traits need more attention (Stratonovich *et al.*, 2012).

Traits associated with growth post-winter frequently co-occurred with early growth traits, suggesting that they represent a suite associated with early vigour, development and

conserved tillering. Multivariate analysis shows that these frequently cluster, and that it was related to suppression of *A. myosuroides*, though the relationship is less apparent in colder years and in the field. For example, Duxford has a high RGR_{GA} and RGR_W, is tall as a seedling and has lower maximum stem number and % stem loss than KWS Santiago. More work would be needed to understand if this suite exists, and how it interactions with environmental conditions and with different competitive scenarios.

7.2.3 Interaction between competitive traits and environmental conditions

No traits were associated with suppressive ability in the same way across all studies. This is due to the interaction of the expression of these traits with a variable environment, something that these studies could only partly capture. Such results are common in *in situ* competition studies and may be attributed to annual differences in rainfall and temperature (Coleman *et al.*, 2001; Mennan & Zandstra, 2005). However, the findings allow for some preliminary conclusions.

Early aboveground weight and green area were important for suppressive ability in both container-based experiments and in the field. However, whilst these traits were important in higher values in the container, greater green area and aboveground weight saw a reduced suppressive ability in the field. This discrepancy may be explained by the negative relationship between these traits and root weight ratio. Different resources could be limited in the field when compared to the containers. The containers were watered, whilst the field was rain-fed. Limited soil moisture or nutrients could mean higher root volume is important for suppression of a weed in the field. Another explanation may be that the containers restricted root

growth, meaning that the differences between cultivars were restricted belowground, leaving aboveground to be the key driver of suppressive ability. However, these are speculations in need of further research.

The container experiment offers some insight into the importance of temperature. Many traits differed in their level of importance across different experimental years, where temperature was one of the main uncontrolled variables. In the warmer autumns and winters, the cultivars were visibly different, and had the greatest differences in traits such as early height and green area. Greater accumulated thermal time coincided with an impact of early-emerging traits on *A. myosuroides* productivity. This was most apparent with early height, which was a good predictive trait in the two warmer years. This effect would also be seen when cultivars are sown earlier, as the crop would have a longer period of time prior to dormancy to develop. Competitive differences between cultivars sown later appeared to be related to traits that emerged post-winter, which would support this hypothesis.

Though the container-based experiment was devised to simulate in-field conditions as closely as possible whilst allowing for some control of extraneous variables, the evidence suggests that it cannot simulate *in situ* competition adequately. The two different experiments may have inadvertently granted insight into competitive dynamics under different scenarios, but these need to be examined in a more thorough manner than the data can allow. An understanding of competition in the field, and if belowground resources are more limiting under competitive scenarios, would be beneficial. Satorre and Snaydon (1992) reported that belowground competition was greater than aboveground in wheat – *Avena fatua* scenarios. Investigating

belowground competition may also require an understanding of other external conditions that influence competition, such as precipitation. Traits that are more appropriate for competition under well-watered scenarios may prove detrimental if water is scarce. If there is a trade-off between green area and root weight, greater green area would be a benefit or a detriment depending on water availability.

7.3 Tolerance traits in wheat

Though suppressive traits have been quantified and discussed in this thesis, tolerance traits proved to be more elusive. No trait could be related to tolerance across both study years (Table 7.2). There was some suggestion that the cultivars that were the best and worst tolerators maintained that position across both years, but differences were limited and lacked statistical significance.

There is a suggestion that 'tolerance to weed competition' does not exist as a suite of traits. Instead, traits that may be associated with tolerance are instead 'stress-resistance' traits (Wang *et al.*, 2010). If this were true, the traits associated with tolerance are those that resist the particular resource pressure that the weed species is exerting. This finding could be supported by 2012-13 data, where resistance to stem loss resulted in higher yield retention. There may have been an increased risk of stem loss in this year due to higher densities of *A. myosuroides* competing for water, which was likely in deficit due to a dry winter and spring.

Table 7.2 – Pearson's correlation coefficients for cultivar traits versus measures of tolerance in the field experiments.

		2013-2014	
Cultivar traits	2012-2013	Early drill	Late drill
Early aboveground weight	**-0.459***	-0.2045	0.4327
Final stem count	**0.5142***	**-0.3995***	**0.5287***
Early leaf area	**0.4164***	-0.1216	0.0841
Early green area	**0.4393***	-0.1482	0.0871
% stem loss	**-0.4483***	0.2851	-0.3644

7.4 **Integrating cultivar choice with IWM strategies**

All cultivars used in this study benefitted from being present at a higher density – a finding supported both in containers, *in silico*, and in a recent meta-analysis (Lutman *et al.*, 2013). There was no significant interaction between cultivar and sowing density. INTERCOM predicted that a suppressive cultivar could be sown at much lower densities than a poor suppressor and provide equivalent control, though this would benefit from validation *in situ*. Increased sowing rate is a popular tool employed by farmers, and its compatibility with cultivar choice is promising.

Suppressive traits were harder to define at lower densities, which could imply that their singular impacts on *A. myosuroides* were limited when the canopy is open for longer and light is more available. However, the suppressive rankings of cultivars changed little. The approximate stability of cultivar ranking across both densities may be because the cumulative effects of these traits allowed cultivars to maintain their ranking at low densities.

In silico experimentation found that the two extreme-ranking cultivars maintained their ranking at different drilling dates, and a more suppressive cultivar sown early could have equivalent control to a less suppressive cultivar sown a month later. *In situ*

experimentation demonstrated that most cultivars achieve higher levels of *A. myosuroides* suppression (seed return plant^{-1}) when drilled later. However, reality is more complicated than the *in silico* experiment implied. A decreased seed return return per plant would be anticipated, as *A. myosuroides* has less time to tiller. In addition, differences in the ability of cultivars to suppress *A. myosuroides* appear when drilled later. For cultivars sown later, the importance of competition at later stages of development is amplified. Earlier traits become less important, whilst lower final stem number becomes an indicator of suppressive ability. This could not be adequately captured by the INTERCOM model, as it does not consider the impact of belowground traits in sufficient detail and predictions are heavily dependent on early growth and development traits.

For example, cultivar Claire is a noteworthy example of behaviour that the model may not anticipate, as its suppressive ability remained equivalent at both drill dates. Claire is recommended for early drilling, suggesting that this cultivar is unable to develop appropriately if drilled later, allowing *A. myosuroides* to outcompete it. It produces a high number of stems, which may mean fewer resources were allocated belowground. As previously discussed, belowground resources may drive competitive success in the field. If Claire initially favours allocating resources to tillers at the expense of roots, it may not have the opportunity to develop sufficient root volume prior to booting when it is sown later. However, it is difficult to draw conclusions from a single experiment and without more detail on belowground traits.

7.5 Stem production and loss

There is no consensus on the importance of stems (most frequently described as tillers) in the literature on crop

competition (Wicks *et al.*, 1986; Lemerle *et al.*, 1996; Didon & Bostrom, 2003). Parameters derived from the split-line model and their relationship to suppressive and tolerance only confirmed that there is no simple answer to its importance in competitive scenarios. In suppression, a general trend is suggested by the container experiment, with a cultivar with a lower maximum stem number, a lower stem loss and a higher final stem number being indicative of a more suppressive strategy. However, all three traits were never related to seed return in any single experiment.

In this thesis, it is suggested that a conserved tillering strategy is appropriate in a more suppressive cultivar, perhaps due to resources being allocated to other traits. Further research into tiller production and loss dynamics under different scenarios would have value. For example, it has been suggested that tillers are more important at low stand density (Challaiah *et al.*, 1986). However, in this study no stem parameters were related to *A. myosuroides* seed production in the low density treatment.

7.6 Predicting suppressive ability

Traits have been identified as suppressive, and that they may vary across years for reasons that are not fully understood. This reinforces the need for a means of screening for cultivar competitive ability that uses a selection of traits, in order to have a reliable ranking of cultivars. Traits that are easier to measure are of greatest value (Hansen *et al.*, 2008).

Early height would be one such trait, but requires a set time at which measurements are taken. Thermal time was used to extrapolate an equivalent measure of height across experiments, but this is not practical for screening. The 3-leaf stage (GS13) would be recommended, which is typically

achieved around the time that early height was quantified in this thesis. Simple measures of leaf number, length and width may sufficiently capture green area. Many of the valuable traits can be captured via high-throughput field phenotyping, such as those employed by breeders'. Plant height may be quantified using LIDAR, shoots m^{-2} through stereo-imaging systems and canopy green area using aerial imaging techniques.

However, the uncertainty surrounding early aboveground weight and early green area presents problems for using these, or derivatives of these, as indicator traits. Greater green area may be a suppressive characteristic in well-watered scenarios and a poor suppressor under water-scarcity, and it would be difficult to determine whether above or belowground competition will be more important in a given season.

Later traits may also be quantified for a screening protocol. The importance of rapid development could also be useful in determining cultivar competitive ability. Maturity is already measured as part of UK recommended list trials, and may serve as a surrogate for time of spike emergence. On the other hand, if an understanding of the importance of tillers to competitive ability can be attained, it is still unlikely that the parameters measured in this study could be used as they cannot be quantified readily. Final stem counts, which were typically conducted during wheat heading, is the exception to this.

Aboveground competition could be summarised as improved light capture at the expense of rival plants. With this in mind, it may be possible to summarise the combined impact of all competitive traits identified in this thesis with a measure of canopy area and light capture. Didon & Hansson (2002) noted that PAR interception was higher in cultivars with greater

suppressive ability. There are numerous canopy sensors available for purchase, and if their values of canopy cover were to be related to suppressive ability and tolerance, this would be the simplest option to determine the competitive ability of a cultivar. The quantification of canopy area and PAR interception was not possible in this study. Measures of canopy cover and their relationship with competitive cultivars and traits could benefit from further study.

7.7 Breeding and trade-offs

Breeding efforts in the UK have traditionally focused on maximising yield potential in near-optimal conditions. This has resulted in a range of commercial cultivars that have low genetic diversity, thus a restricted range of physiological traits. Many researchers are now interested in the genetic diversity of wheat, hoping to find traits that may prove beneficial in various scenarios, such as those predicted with climate change. Such work could see cultivars with enhanced competitive ability being developed, which may become increasingly important as herbicide efficacy decreases.

Potential target traits have been identified in this studentship, but there still exists a concern of possible trade-off with weed-free yield potential. Height at maturity is considered the archetypal trait that has a trade-off with yield, and was the key to the higher yielding potential of the semi-dwarfs developed during the Green Revolution. There was no evidence of a trade-off between suppressive ability and weed-free yield in this study. Specific leaf area was related to both increased suppressive ability and reduction in weed-free yield, but not in the same experiment. But since weed-free yield could only be examined in one experiment, a potential trade-off cannot be dismissed.

Within this thesis, competition has been near-exclusively discussed in an interspecific context. As many traits have been measured at the level of the individual, it would be naïve to assume that they do not result in intraspecific competition. The traits are likely to target neighbouring individuals of the same species, due to their very similar resource requirements, and so may indicate an investment in competition that is not refined to maximise the yield of the population. A case has been made for group selection in breeding for competitive ability (Denison, 2012). The key principle is that the traits and the yield of the whole crop stand be considered, rather than the individual. Individual plants often benefit by outstripping neighbours resources, which could lead to overall decrease in yield. This principle has been termed "Tragedy of the Commons". Group selection may allow for co-operative traits to be selected that would not normally be favoured in aggregated populations of wheat. Vigorous early growth and greater initial size (in combination with a more uniform spatial sowing pattern) in wheat has been suggested as a target for co-operative suppression through the early smothering of weeds (Weaver *et al.*, 2010). It has been suggested that the development of semi-dwarf cultivars was an example of selection for more co-operative cultivars, as natural selection favoured taller mature cultivars in order for them to compete with their neighbours (Denison, 2012). One possible example is the proposed ability of some cultivars to detect the root systems of neighbours and alter root growth to avoid intraspecific competition (Zhu & Zhang, 2013), or a cultivar only expressing competitive traits when in the presence of weeds.

7.8 Conclusions and further studies

This study has provided evidence of traits that are related to suppressive ability, with rapidly developing cultivars with a conserved tillering strategy being the more suppressive. Tolerance traits were more difficult to identify, but tolerance and suppressive ability were frequently related. Some traits may be used to predict suppressive ability of cultivars, but their importance will depend on weather conditions and the local environment. Cultivar choice was highly compatible with other weed control strategies, though evidence suggests that some cultivars perform poorly when drilling is delayed.

What became most apparent during this studentship was the complicated nature of the traits involved in competitive interactions. Although a rapidly developing ideotype may be recommended, further research would be required to better quantify this potential ideotype, its genetic basis and how it responds to different conditions. There are various other topics that may be recommended for further study. A selection of topics worthy of further study are outlined below.

1. Belowground traits

Cultivars with competitive belowground traits would be of particular value under soil moisture and nutrient-limited environments. Traits of potential value could include rooting depth, distribution with depth, surface area, and the identity and combinations of allelopathic exudates. There are inherent difficulties investigating belowground competition, but as techniques improve their assessment is likely to become easier to quantify.

2. Tillering

Stem production and loss, and parameters related to these dynamics, are influenced by both genetics and the environment. These need to be adequately understood in the context of competition. Once the value of these parameters is better understood, their interaction with other external factors (such as plant density), can be ascertained.

3. Weed specificity

In this study, attempts to examine suppression of *A. mysoroides* and *S. media*, and the traits responsible, failed to generate meaningful results. Knowledge of weed specificity would make it known if suppressive rankings derived from one species may be applicable to other weed species. It would also have value for farmers who must manage multiple problematic weed species.

4. Trait heritability and trade-offs

To encourage selection for competitive cultivars, it would be beneficial to know the heritability of key competitive traits and if they have trade-offs with other, high value traits (particularly those associated with yield potential). Some work has been done in this area (e.g. Coleman *et al.*, 2001). This understanding may not need to be researched explicitly – rather, the information may already exist in the growing body of literature on wheat genetic variability.

5. Red:far-red light ratios and weed partitioning

Early traits may affect red:far-red light ratios, and so stimulate a shade avoidance response in *A. myosuroides*. If this occurs, these early traits could reduce *A. myosuroides* seed return before true competition begins. Experiments are required to determine the existence, and extent, of a shade avoidance

response, and if the suppressive ability of early traits in this study may be associated with red-far:red light ratios.

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9 Appendices

Table App.1 - The fungicide programmes used in the sand-beds experiments

Treatment	Fungicide	Quantity per litre	Date/s applied (2011-12)	Date/s applied (2012-13)	Date/s applied (2013-14)
Winter mildew treatment	Corbel	1.0 ml	14-11-2011 and 23-01-2012	08-01-2013	05-12-2013 and 02-02-2014
	Fortress	1.0 ml			
T0	Cherokee	1.9 ml	28-02-2012	16-04-2013	11-03-2014
	Flexity	0.5 ml			
T1	Proline	1.8 ml	04-04-2012	17-05-2013	11-03-2014
	Bravo	2.5 ml			
	Talius	0.38 ml			
T2	Opus	1.9 ml	30-04-2012	07-06-2013	24-04-2014
	Comet	1.9 ml			

Table App. 2 - Details on management of the 2012-13 field experiment.

Date	Application	Rate/Units	Notes
02/10/2012	Marked and Drilled Experiment	all sept varieties - see plan	
18/10/2012	Spread Slug Pellets	Gusto @ 6kgs/ha	
14/11/2012	Sprayed Glyphosate	@2.0lt/ha	ONLY ONTO OCT PLOTS
02/03/2013	Spring Tyned	Undrilled Plots Only.	
06/04/2013	Drilled Surrounds Only with Xi19/Crusoe	@450sm2	
16/04/2013	Applied DoubleTop Fertilizer	@222kg/ha	
25/04/2013	Sprayed Atlantis and Bio Power	As Plan	AT@0.4 and BP@1.0lt/ha
30/04/2013	Applied Nitram	@290kg/ha	
07/05/2013	Sprayed Kingdom and Bravo	Kingdom@1.25lt/ha and Bravo@1.0lt/ha	
02/06/2013	Sprayed Refine Max, Competox+, kingdom, bravo 500	ref@75g, com@1.0l, kin@1.25l, brav@1.0l - ha	
21/06/2013	Cut paths	.	
04/07/2013	Electric Fence Removed	.	
09/07/2013	Cut/Cultivated Paths	.	
19/08/2013	Sampo - Harvested	.	
20/08/2013	Sampo - Harvested	.	
20/08/2013	Sprayed Samurai	@4lt/ha	
21/09/2013	Sprayed Round Up Max	@0.75ml/ha	

Table App. 3 - Details on the management of the 2013-14 field experiment

Date	Application	Rate/Units	**Notes**
04/10/2013	Drilled all varieties	October Plots - All Drilled to plan	
04/10/2013	Drilled	All plots to plan + immediate surrounds	
15/10/2013	Applied Major Slug Pellets	@4kg/ha	
24/10/2013	Drilled 2nd Sowing	October Plots - All Drilled to plan	
05/11/2013	Applied Rabbit Fence	-	
13/11/2013	Sprayed Hallmark + Pixie	Hal@50ml + Pix@1.5lt/ha	
06/03/2014	Applied Double Top Fertilizer	@222Kg/Ha	
28/03/2014	Sprayed Artemis and Bravo 500	Both @1lt/ha	
02/04/2014	Applied Nitram Feriliser	@290kg/ha	
23/04/2014	Apllied Nitram	@145kg/ha	
28/04/2014	Sprayed Ally Max, Kingdom, Bravo + Hatchet Xtra	ally@30grm, king@1.25lt, bra@1.0lt, Hatc@1.0lt/ha	
16/05/2014	Sprayed Vortex	@1.5lt/ha	
20/05/2014	Cut Paths	Topper 9 and GPS	
30/05/2014	Sprayed Brutus and Curator	Bru@1.5lt and Cur@1.0lt - ha	
02/06/2014	Topped All Paths	With GPS and Topper 9	
16/06/2014	Cut Paths	GPS and topper 9	
17/07/2014	Cut Paths and Surrounds	.	
21/07/2014	Cut Paths	.	
20/08/2014	Sampo Harvested	All Wheat Plots	

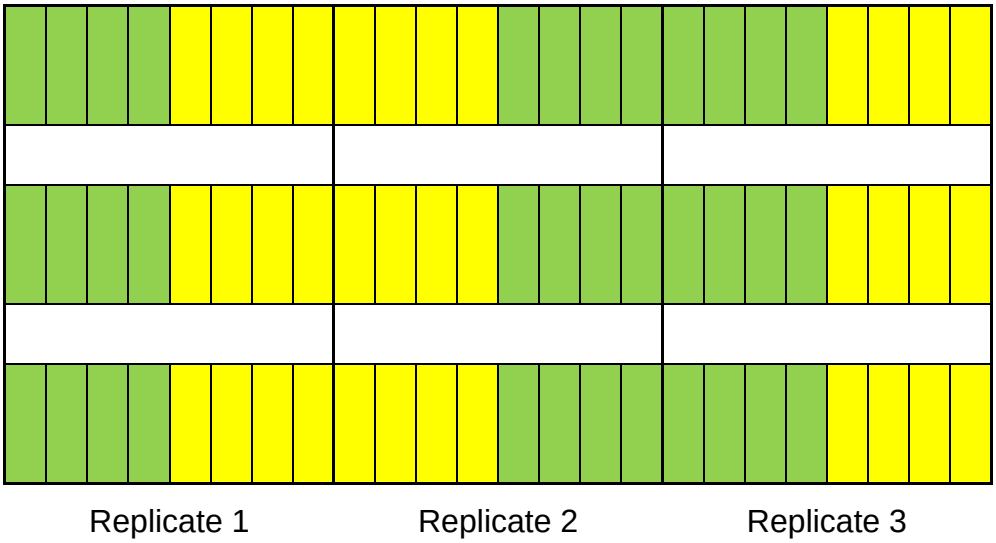

Figure App. 1 - The layout of the field experiment in 2013-14. The 2012-13 was arranged similarly. Yellow denotes early sown plots, green denotes late sown plot. Each marked plot was divided into 'weedy' and 'weed-free' subplots.

Table App. 4 - Mean trait values of wheat cultivars in the sand-bed based experiments

Cultivar traits	Sand-beds 2011-12		Sand-beds 2012-13 (*A. myo)*		Sand-beds 2012-13 (*S. media)*		Sand-beds 2013-14 High density		Sand-beds 2013-14 Low density	
	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Ear index	n/a		n/a		n/a		n/a		n/a	
Flag leaf length (mm)	195.1	5.383	123.7	3.020	123.4	3.315	163.4	4.583	176.0	4.717
Flag leaf width (mm)	17.4	0.342	14.8	0.213	15.0	0.122	17.1	0.329	17.9	0.288
Flag leaf area (mm^2)	n/a		1409.7	51.737	1485.6	67.832	2071.1	117.156	2144.1	116.190
Flag leaf SLA (m/g)	n/a		n/a		0.015	0.00036	0.017	0.00031	0.018	0.00038
Flag leaf angle (^{0})	n/a		21.8	0.891	21.1	0.703	22.5	2.481	23.3	2.373
Early leaf number	8.2	0.371	6.3	0.179	6.3	0.216	3.2	0.060	3.1	0.061
Early height (mm)	102.5	5.649	78.2	2.292	84.3	3.197	95.7	2.134	94.3	1.869
Final height (mm)	805.7	23.653	608.5	10.410	601.6	8.522	711.9	11.326	735.6	10.817
Time of max. growth rate (ptt)	951.7	27.171	814.0	22.575	777.1	14.338	885.4	18.534	876.4	17.185
Final stem count	n/a		1.7	0.084	n/a		1.7	0.120	2.4	0.131
% Stem loss	n/a		64.1	1.568	n/a		64.4	2.224	59.7	2.327
Time of max. stem no. (ptt)	235.7	13.307	591.8	25.261	n/a		255.4	10.854	300.1	11.317
Max stem number	5.4	0.530	4.9	0.179	n/a		5.2	0.311	6.3	0.394
Rate of tillering (stem/ptt)	0.0331	0.00215	0.0088	0.00073	n/a		0.0260	0.00127	0.0258	0.00133
Weed-free yield (kg m^2)	n/a		n/a		n/a		n/a		n/a	
Maximum growth rate (mm/ptt)	1.02	0.0640	1.30	0.0643	n/a		0.98	0.0656	1.00	0.0591
75% spike emergence (ptt)	n/a		913.5	4.13	912.2	4.01	863.4	7.73	863.4	8.29
Early leaf length (mm)	n/a		113.6	2.80	112.4	3.26	97.2	1.78	98.2	2.00

Early leaf width (mm)	n/a		4.81	0.148	4.67	0.121	5.12	0.218	5.05	0.213
Early leaf angle (^{0})	n/a		37.2	2.41	41.4	2.16	46.7	2.19	48.8	1.94
50% emergence (DAS)	10.9	0.24	8.4	0.15	8.3	0.13	7.6	0.08	7.5	0.10
$RGRG_{DWT}$ (g^{-1} g^{-1} tt^{-1})	0.0072	0.00018	0.0062	0.00022	0.0062	0.00022	0.0083	0.00015	0.0083	0.00015
RGR_{GA} (cm^{-2} cm^{-2} tt^{-1})	0.0116	0.00041	0.0091	0.00033	0.0091	0.00033	0.0089	0.00024	0.0089	0.00024
LAR	199.9	10.90	93.6	3.39	93.6	3.39	122.7	3.66	122.7	3.66
LWR	0.42	0.0086	0.31	0.0056	0.31	0.0056	0.40	0.0062	0.40	0.0062
NAR (g m^{-2} d^{-1})	0.42	0.033	0.89	0.035	0.89	0.035	0.78	0.022	0.78	0.022
RWR	0.26	0.005	0.39	0.009	0.39	0.009	0.26	0.008	0.26	0.008
Early green area (mm^2)	25.7	2.404	8.8	0.338	8.8	0.338	11.1	1.061	11.1	1.061
ABGW (g)	0.070	0.0053	0.047	0.0026	0.047	0.0026	0.063	0.0054	0.063	0.0054
Early SLA (m/g)	0.0477	0.0018	0.03179	0.0014	0.03179	0.0014	0.0319	0.00075	0.0319	0.0008
TGW (g)	45.9	1.716	41.8	1.297	41.8	1.297	38.0	1.193	37.2	1.193

Table App. 5 - Mean trait values of wheat cultivars in the field experiments

	In-field 2012-13		In-field 2013-14 Late drill		In-field 2013-14 Early drill	
Cultivar traits	Mean	±	Mean	±	Mean	±
Ear index	34.6	1.196	52.9	1.195	37.2	1.552
Flag leaf length (mm)	184.9	2.956	196.5	2.731	191.9	3.017
Flag leaf width (mm)	16.1	0.195	17.9	0.177	17.9	0.207
Flag leaf area (mm^2)	2444.4	78.401	2578.0	71.609	2660.2	74.039
Flag leaf SLA (m/g)	0.027	0.00050	0.025	0.00035	0.024	0.00024
Flag leaf angle	29.8	0.964	16.0	0.959	17.0	0.740
Early leaf number	5.4	0.172	5.6	0.173	9.9	0.322
Early height (mm)	78.2	1.800	88.3	1.222	107.3	2.083
Final height (mm)	725.4	8.491	906.7	9.605	907.7	11.305
Time of max. growth rate (ptt)	847.4	28.176	769.7	7.360	1059.2	13.557
Final stem count	1.9	0.073	3.1	0.083	2.5	0.049
% Stem loss	32.6	2.244	5.3	4.738	37.1	1.670
Time of max. stem no. (ptt)	547.3	48.755	461.0	31.284	369.4	13.909
Max stem number	2.9	0.113	3.2	0.088	4.1	0.085
Rate of tillering (stem/ptt)	0.0071	0.001291	0.0068	0.000401	0.0146	0.00083
Early green area (mm)	7.4	0.343	11.5	0.409	21.9	1.013
ABGW (g)	0.047	0.0019	0.084	0.0026	0.136	0.0055
Early SLA (m/g)	0.0259	0.00041	0.0249	0.00027	0.0269	0.00042
TGW (g)	41.8	0.722	37.6	0.540	37.6	0.540

Table App. 6a - Mean traits values for cultivars in the sand-bed experiment 2011-12

	Claire		Conqueror		Denman		Duxford		Gallant		Gerald	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Seed return (plant^{-1})	2907	190.99	1941	270.48	2644	130.57	1938	204.69	2272	145.96	3336	226.54
weed biomass (g plant^{-1})	15.9	1.61	11.4	1.41	14.2	0.30	10.4	0.94	11.6	0.69	18.3	1.17
Final height (mm)	818	29.42	790	14.94	748	8.70	812	16.04	778	20.53	974	15.86
Time of max. growth rate	1052	20.85	944	21.55	954	52.83	891	95.73	958	2.73	946	38.86
Maximum growth rate	1.12	0.0099	0.88	0.0131	0.96	0.0938	0.84	0.0298	0.95	0.0136	1.51	0.1527
Early height (mm)	95.0	1.64	99.3	3.10	103.9	1.25	116.3	4.04	101.4	3.93	88.4	1.74
Rate of tillering (stems ptt)	0.029	0.00101	0.030	0.00172	0.031	0.00148	0.029	0.00256	0.031	0.00129	0.025	0.00520
Maximum stem number	4.3	0.13	4.6	0.18	4.8	0.45	3.6	0.34	4.5	0.51	4.9	0.87
Time of max. stem number	213	4.41	225	1.41	227	5.06	194	6.05	218	12.11	283	68.87
Flag leaf length (mm)	184.1	4.07	194.9	3.93	220.7	4.05	213.6	4.22	185.2	1.01	161.2	3.42
Flag leaf width (mm)	17.4	0.56	17.7	0.32	16.3	0.52	19.2	0.07	16.4	0.25	15.5	0.72
Early leaf counts	7.9	0.48	7.8	0.11	7.8	0.44	7.8	0.78	8.0	0.33	7.1	0.40
50% emergence (DAS)	10.3	0.33	10.3	0.33	10.7	0.33	11.3	0.33	11.3	0.67	10.7	0.67
TGW (g)	43.4	n/a	40.0	n/a	44.4	n/a	48.8	n/a	50.3	n/a	33.1	n/a
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0076	n/a	0.0067	n/a	0.0081	n/a	0.0083	n/a	0.0078	n/a	0.0073	n/a
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0123	n/a	0.0111	n/a	0.0124	n/a	0.0146	n/a	0.0117	n/a	0.0094	n/a
SLA	0.0464	n/a	0.0487	n/a	0.0453	n/a	0.0478	n/a	0.0500	n/a	0.0384	n/a
LAR	202.6	n/a	197.9	n/a	199.5	n/a	204.3	n/a	199.6	n/a	157.3	n/a
LWR	0.424	n/a	0.402	n/a	0.427	n/a	0.407	n/a	0.397	n/a	0.415	n/a
NAR	0.410	n/a	0.363	n/a	0.452	n/a	0.507	n/a	0.390	n/a	0.653	n/a
ABGW (g)	0.060	n/a	0.076	n/a	0.053	n/a	0.068	n/a	0.079	n/a	0.050	n/a
RWR	0.251	n/a	0.265	n/a	0.270	n/a	0.252	n/a	0.240	n/a	0.262	n/a
Early green area (cm^2)	22.3	n/a	28.9	n/a	18.0	n/a	24.5	n/a	27.7	n/a	17.5	n/a

Table app. 6b - Mean traits values for cultivars in the sand-bed experiment 2011-12.

	Grafton		Invicta		Ketchum		Kingdom		KWS Santiago		Maris Widgeon	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Seed return (plant^{-1})	3122	367.39	2518	201.85	2337	201.31	2816	105.02	3007	110.09	1529	312.78
weed biomass (g plant^{-1})	17.4	1.92	12.3	0.92	13.4	1.17	17.2	0.79	16.4	1.11	7.4	1.62
Final height (mm)	690	8.21	804	10.00	815	15.25	855	32.49	873	24.77	1001	21.00
Time of max. growth rate	902	102.27	935	35.88	1054	11.60	989	45.99	948	85.23	1084	15.72
Maximum growth rate	0.97	0.0681	0.93	0.0302	1.13	0.0862	1.19	0.1001	1.05	0.0806	1.39	0.0208
Early height (mm)	94.2	4.79	88.9	0.59	106.7	6.80	102.8	4.46	89.6	3.71	126.8	7.16
Rate of tillering (stems ptt)	0.034	0.00733	0.028	0.00009	0.028	0.00135	0.027	0.00919	0.037	0.00456	0.031	n/a
Maximum stem number	8.0	0.28	5.0	0.06	4.3	0.17	5.5	0.50	5.9	0.35	4.3	n/a
Time of max. stem number	309	47.44	248	1.31	225	6.69	291	73.73	243	25.93	193	n/a
Flag leaf length (mm)	185.1	7.16	206.3	2.65	222.0	4.24	155.6	9.04	210.4	9.02	247.5	13.74
Flag leaf width (mm)	17.6	0.35	19.6	0.38	18.0	0.26	15.6	0.60	17.6	0.25	16.8	0.47
Early leaf counts	9.4	0.78	7.3	0.33	8.0	0.00	8.9	0.97	8.3	0.38	n/a	
50% emergence (DAS)	10.7	0.67	11.0	0.58	11.7	0.33	11.0	0.58	11.3	0.67	n/a	
TGW (g)	55.4	n/a	40.2	n/a	50.8	n/a	47.6	n/a	45.6	n/a	n/a	n/a
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0074	n/a	0.0062	n/a	0.0073	n/a	0.0069	n/a	0.0067	n/a	n/a	n/a
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0121	n/a	0.0107	n/a	0.0122	n/a	0.0115	n/a	0.0111	n/a	0.0109	n/a
SLA	0.0467	n/a	0.0468	n/a	0.0478	n/a	0.0478	n/a	0.0447	n/a	0.0500	n/a
LAR	183.7	n/a	198.7	n/a	198.4	n/a	189.7	n/a	186.9	n/a	206.7	n/a
LWR	0.392	n/a	0.415	n/a	0.410	n/a	0.389	n/a	0.423	n/a	0.408	n/a
NAR	0.453	n/a	0.365	n/a	0.421	n/a	0.396	n/a	0.330	n/a	0.366	n/a
ABGW (g)	0.068	n/a	0.054	n/a	0.056	n/a	0.068	n/a	0.059	n/a	0.088	n/a
RWR	0.263	n/a	0.257	n/a	0.256	n/a	0.249	n/a	0.280	n/a	0.245	n/a
Early green area (cm^2)	24.5	n/a	19.3	n/a	21.2	n/a	23.2	n/a	21.4	n/a	30.2	n/a

Table App. 6c Mean traits values for cultivars in the sand-bed experiment 2011-12.

	Oakley		Robigus		Sequel		Suzuka		SY Epson		Torphins		Volume	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Seed return (plant^{-1})	2222	195.18	2188	202.86	649	63.79	2625	288.31	2625	288.31	2995	124.00	696	27.59
weed biomass (g plant^{-1})	10.6	0.75	11.7	1.71	7.1	1.39	2.9	0.39	12.3	0.38	16.9	1.27	3.1	0.01
Final height (mm)	765	7.89	750	18.18	n/a		n/a		765	45.58	783	3.30	n/a	
Time of max. growth rate	953	9.87	972	23.52	n/a		n/a		932	31.74	998	10.83	n/a	
Maximum growth rate	0.89	0.0468	0.94	0.0726	n/a		n/a		1.66	0.0230	1.06	0.0836	n/a	
Early height (mm)	99.7	4.17	88.1	2.91	128.9	7.24	190.0	6.81	99.7	3.69	70.8	7.67	153.2	0.91
Rate of tillering (stems ptt)	0.032	0.00271	0.033	0.00205	0.037	0.00313	0.037	0.00123	0.033	0.00051	0.037	0.00095	0.048	0.00155
Maximum stem number	4.6	0.46	4.6	0.39	7.9	0.85	11.0	0.34	5.0	0.10	5.3	0.23	9.4	0.18
Time of max. stem number	222	10.32	216	7.74	290	29.82	362	6.52	218	5.31	224	7.95	275	4.50
Flag leaf length (mm)	209.4	3.36	212.3	5.31	n/a		n/a		220.0	10.46	194.8	7.56	n/a	
Flag leaf width (mm)	16.6	0.17	18.2	0.42	n/a		n/a		17.9	0.22	17.9	0.32	n/a	
Early leaf counts	7.3	0.33	7.6	0.40	9.0	0.38	10.6	1.11	8.6	0.59	8.3	0.33	10.8	0.56
50% emergence (DAS)	10.7	0.33	11.3	0.33	10.7	0.33	10.7	0.33	10.3	0.33	11.7	0.33	n/a	
TGW (g)	50.1	n/a	47.2	n/a	37.8	n/a	56.2	n/a	51.3	n/a	47.7	n/a	45.5	n/a
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0071	n/a	0.0069	n/a	0.0073	n/a	0.0079	n/a	0.0078	n/a	0.0069	n/a	0.0064	n/a
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0123	n/a	0.0111	n/a	0.0098	n/a	0.0106	n/a	0.0125	n/a	0.0114	n/a	0.0104	n/a
SLA	0.0452	n/a	0.0492	n/a	0.0593	n/a	0.0634	n/a	0.0495	n/a	0.0462	n/a	0.0596	n/a
LAR	181.8	n/a	195.6	n/a	292.4	n/a	300.1	n/a	207.7	n/a	181.7	n/a	289.6	n/a
LWR	0.411	n/a	0.393	n/a	0.494	n/a	0.474	n/a	0.394	n/a	0.401	n/a	0.488	n/a
NAR	0.405	n/a	0.404	n/a	0.307	n/a	0.375	n/a	0.436	n/a	0.383	n/a	0.290	n/a
ABGW (g)	0.060	n/a	0.057	n/a	0.108	n/a	0.150	n/a	0.068	n/a	0.063	n/a	0.118	n/a
RWR	0.264	n/a	0.266	n/a	0.235	n/a	0.224	n/a	0.240	n/a	0.254	n/a	0.229	n/a
Early green area (cm^2)	20.6	n/a	21.5	n/a	45.6	n/a	64.3	n/a	24.0	n/a	20.9	n/a		n/a

Table App. 7a - Mean traits values for cultivars in the sand-bed *S. media* experiment 2012-13.

	Claire		Conqueror		Duxford		Grafton	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	621.0	32.49	590.2	2.61	643.5	20.74	522.7	14.94
Time of max. growth rate (ptt)	829	26.0	681	68.8	765	88.7	712	19.7
Early height (mm)	90.8	4.37	77.0	5.17	108.5	5.85	65.7	8.17
75% spike emergence (ptt)	922	10.8	891		917	20.9	908	12.7
Flag leaf angle (^{0})	24.3	1.47	17.4	3.92	20.5	1.88	19.4	2.55
Flag leaf length (mm)	124.5	6.51	132.9	13.31	116.2	13.31	95.6	1.27
Flag leaf width (mm)	15.1	0.17	15.2	0.57	14.7	0.08	14.3	0.12
Flag leaf area (mm^2)	1441	127.8	1561	208.5	1360	141.2	1005	6.2
Flag leaf SLA (m/g)	0.0163	0.00042	0.0170	0.00087	0.0167	0.00038	0.0150	0.00055
Early leaf counts	6.4	0.56	7.3	0.27	4.7	0.00	7.0	0.33
Early leaf length (mm)	110.2	7.31	132.9	1.04	121.8	8.94	102.0	10.78
Early leaf width (mm)	4.9	0.29	4.9	0.23	5.2	0.04	4.1	0.41
Early leaf angle (^{0})	25.3	4.24	45.8	0.54	26.3	4.76	36.9	1.35
50% emergence (DAS)	8.0	0.58	8.0	0.00	9.0	0.00	8.7	0.33
TGW (g)	50.1		41.5		35.8		41.2	
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0069		0.0050		0.0064		0.0064	
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0098		0.0081		0.0108		0.0081	
SLA	0.0425		0.0324		0.0319		0.0327	
LAR	95.3		100.4		107.0		70.9	
LWR	0.286		0.311		0.329		0.288	
NAR	0.90		0.80		0.86		0.82	
ABGW (g)	0.051		0.044		0.047		0.043	
RWR	0.410		0.404		0.372		0.405	
Early green area (cm^2)	9.9		8.6		10.1		8.6	

Table App. 7b - Mean traits values for cultivars in the sand-bed *S. media* experiment 2012-13.

	Hereward		KWS Santiago		Oakley		Panorama		Robigus	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	620.4	18.64	644.1	10.87	574.5	4.31	624.2	23.36	584.2	21.60
Time of max. growth rate (ptt)	785	59.43	828	29.41	760	36.88	837	23.51	761	19.95
Early height (mm)	90.8	1.64	66.4	5.25	81.9	10.01	106.7	4.88	77.0	3.09
75% spike emergence (ptt)	925	9.9	913	16.2	917	18.0	901		910	17.9
Flag leaf angle (^{0})	19.0	1.97	20.1	2.23	21.6	2.21	23.3	0.82	23.0	2.58
Flag leaf length (mm)	111.7	10.91	142.8	1.66	134.1	3.23	128.4	10.07	128.9	4.07
Flag leaf width (mm)	15.0	0.20	14.6	0.38	16.3	0.08	14.8	0.17	15.7	0.19
Flag leaf area (mm^2)	1347	185.7	1636	36.5	1714	26.0	1347	215.7	1611	35.2
Flag leaf SLA (m/g)	0.0159	0.00268	0.0132	0.00032	0.0140	0.00029	0.0134	0.00017	0.0144	0.00029
Early leaf counts	6.6	1.09	6.3	0.77	5.7	0.19	7.0	0.96	5.9	0.56
Early leaf length (mm)	119.4	15.30	105.7	15.56	104.6	5.27	121.8	11.29	103.1	6.32
Early leaf width (mm)	4.8	0.31	3.7	0.31	4.5	0.19	5.4	0.48	4.6	0.04
Early leaf angle (^{0})	52.9	2.17	40.7	1.11	36.8	1.75	52.1	4.79	63.8	3.33
50% emergence (DAS)	8.0	0.00	8.0	0.00	9.0	0.00	7.7	0.33	8.3	0.33
TGW (g)	41.4		38.2		47.0		42.7		40.4	
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0073		0.0060		0.0064		0.0064		0.0052	
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0081		0.0086		0.0105		0.0091		0.0081	
SLA	0.0295		0.0295		0.0265		0.0327		0.0314	
LAR	99.7		88.8		83.8		104.9		93.7	
LWR	0.343		0.308		0.307		0.323		0.301	
NAR	1.04		0.85		1.14		0.79		0.84	
ABGW (g)	0.068		0.041		0.043		0.045		0.041	
RWR	0.320		0.402		0.400		0.380		0.419	
Early green area (cm^2)	10.2		7.2		7.6		8.9		7.7	

Table App. 8a - Mean traits values for cultivars in the sand-bed (*A. myosuroides*) experiment 2012-13.

	Claire		Conqueror		Duxford		Gallant		Grafton	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	625.3	43.48	575.4	51.92	650.2	13.98	548.7	44.39	581.8	22.15
Time of max. growth rate (ptt)	900	10.9	636	18.8	904	14.7	770	67.6	652	52.3
Maximum growth rate (mm/ptt)	1.75	0.098	0.91	0.131	1.32	0.196	1.00	0.244	1.00	0.117
Early height (mm)	86.0	5.81	76.8	3.13	99.7	1.26	75.8	5.39	66.0	1.84
Final stem count	1.3	0.19	2.0	0.00	1.7	0.19	1.7	0.38	1.9	0.29
Tillering rate (stems/ptt)	0.0070	0.00089	0.0070	0.00064	0.0084	0.00025	0.0063	0.00017	0.0107	n/a
Maximum stem number	4.3	0.56	4.9	0.45	5.2	0.21	4.6	0.36	8.1	n/a
Time of max. stem number (ptt)	579	46.13	663	22.97	633	38.94	710	66.42	682	n/a
% stem loss	69.5	2.36	58.4	4.20	67.7	5.03	56.6	2.50	71.3	n/a
75% spike emergence (ptt)	913	10.80	919	14.95	891	5.83	893	8.00	917	21.61
Flag leaf angle (^{0})	25.7	2.16	18.1	1.14	19.4	2.25	28.9	3.47	23.7	1.97
Flag leaf length (mm)	110.9	14.41	118.3	3.67	123.3	12.67	110.9	4.07	107.9	7.95
Flag leaf width (mm)	15.0	0.17	13.7	0.19	14.0	0.55	13.9	0.43	14.5	0.46
Flag leaf area (mm^2)	1232	264.7	1293	63.7	1449	199.9	1205	47.7	1092	131.9
Early leaf counts	5.8	0.29	6.2	0.22	5.3	0.28	5.2	0.29	7.6	0.71
Early leaf length (mm)	108.4	4.34	119.3	3.11	129.7	10.84	120.6	12.67	100.9	10.92
Early leaf width (mm)	5.3	0.23	4.4	0.22	5.8	0.67	5.3	0.55	4.4	0.66
Early leaf angle (^{0})	34.7	4.12	34.5	6.62	27.4	1.70	27.2	5.26	43.1	8.37
50% emergence (DAS)	8.0	0.58	8.0	0.58	8.7	0.33	9.3	0.33	9.0	0.58
TGW (g)	50.1		41.5		35.8		40.0		41.2	
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0069		0.0050		0.0064		0.0062		0.0064	
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0098		0.0081		0.0108		0.0098		0.0081	
SLA	0.0425		0.0324		0.0319		0.0288		0.0327	
LAR	95.3		100.4		107.0		91.2		70.9	
LWR	0.286		0.311		0.329		0.312		0.288	
NAR	0.90		0.80		0.86		0.91		0.82	
ABGW (g)	0.051		0.044		0.047		0.050		0.043	
RWR	0.410		0.404		0.372		0.367		0.405	
Early green area (cm^2)	9.9		8.6		10.1		9.1		8.6	

Table App. 8b - Mean traits values for cultivars in the sand-bed (*A. myosuroides*) experiment 2012-13.

	Hereward		KWS Santiago		Oakley		Panorama		Robigus	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	596.4	21.72	670.2	4.01	566.9	9.81	654.2	14.41	615.5	13.25
Time of max. growth rate (ptt)	896	8.5	903	13.1	886	11.6	812	91.0	782	78.5
Maximum growth rate (mm/ptt)	1.14	0.115	1.72	0.073	1.35	0.088	1.42	0.131	1.36	0.136
Early height (mm)	79.9	2.92	64.4	5.07	72.3	5.21	85.1	5.91	76.1	9.14
Final stem count	2.0	0.51	1.4	0.22	1.7	0.19	1.6	0.29	1.6	0.11
Tillering rate (stems/ptt)	0.0116	0.00420	0.0157	0.00604	0.0079	0.00071	0.0084	0.00168	0.0076	0.00099
Maximum stem number	4.5	0.84	4.3	0.11	4.9	0.15	4.3	0.41	5.1	0.59
Time of max. stem number (ptt)	455	182.61	384	114.15	602	69.57	501	46.70	660	20.89
% stem loss	48.8	2.49	68.7	7.15	66.2	2.98	66.2	6.26	68.8	2.12
75% spike emergence (ptt)	942	9.32	927	8.08	919	14.95	902	10.80	910	2.29
Flag leaf angle (^{0})	19.5	3.47	17.8	1.14	24.0	3.43	20.1	1.74	20.4	0.42
Flag leaf length (mm)	116.9	1.83	140.4	3.86	129.9	6.63	133.4	3.45	145.4	4.45
Flag leaf width (mm)	16.2	1.25	14.4	0.21	14.9	0.03	15.5	0.22	16.2	0.70
Flag leaf area (mm^2)	1364	5.2	1640	67.3	1443	115.0	1536	65.0	1844	84.1
Early leaf counts	7.5	0.33	6.5	0.42	6.2	0.44	6.7	0.34	5.7	0.45
Early leaf length (mm)	111.6	6.90	103.7	4.12	120.0	9.13	121.7	7.01	100.4	7.80
Early leaf width (mm)	4.6	0.24	4.0	0.27	4.6	0.42	5.2	0.46	4.7	0.24
Early leaf angle (^{0})	38.1	1.88	56.1	6.87	37.0	7.76	29.1	3.78	45.3	13.69
50% emergence (DAS)	8.0	0.00	8.0	0.58	9.0	0.00	7.7	0.33	8.3	0.33
TGW (g)	41.4		38.2		47.0		42.7		40.4	
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0073		0.0060		0.0064		0.0064		0.0052	
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0081		0.0086		0.0105		0.0091		0.0081	
SLA	0.0295		0.0295		0.0265		0.0327		0.0314	
LAR	99.7		88.8		83.8		104.9		93.7	
LWR	0.343		0.308		0.307		0.323		0.301	
NAR	1.04		0.85		1.14		0.79		0.84	
ABGW (g)	0.068		0.041		0.043		0.045		0.041	
RWR	0.320		0.402		0.400		0.380		0.419	
Early green area (cm^2)	10.2		7.2		7.6		8.9		7.7	

Table App. 9a - Mean traits values for cultivars in the sand-bed (high density) experiment 2013-14.

	Claire		Conqueror		Duxford		Gallant		Gerald		Grafton	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	716.3	43.58	738.9	38.17	720.4	25.37	680.5	26.59	808.2	59.73	644.8	19.39
Time of max. growth rate (ptt)	854	26.2	902	27.9	733	193.9	856	56.0	928	28.7	838	14.1
Maximum growth rate (mm/ptt)	1.01	0.097	0.88	0.085	0.81	0.056	0.92	0.062	1.33	0.042	0.83	0.120
Early height (mm)	89.2	9.13	100.4	5.22	110.1	7.22	105.8	7.75	89.4	2.79	89.0	2.04
Final stem count	1.8	0.44	1.9	0.11	1.6	0.29	1.3	0.19	1.9	0.73	1.7	0.19
Tillering rate (stems/ptt)	0.0239	0.00215	0.0196	0.00241	0.0283	0.00417	0.0279	0.00421	0.0227	0.00144	0.0345	0.00277
Maximum stem number	4.8	0.324	4.2	0.077	3.9	0.058	4.3	0.150	8.0	0.536	5.9	0.147
Time of max. stem number (ptt)	255.9	28.49	256.6	23.99	192.7	18.79	208.4	17.27	394.4	0.97	234.3	6.34
% stem loss	61.3	12.08	55.2	3.38	60.4	7.00	69.0	4.31	77.4	7.15	71.7	3.91
75% spike emergence (ptt)	870	17.3	851	18.2	848	19.4	793	38.1	911	13.8	844	19.8
Flag leaf angle (^{0})	27.1	2.98	24.3	4.10	26.6	3.21	30.8	1.10	14.7	0.58	14.8	1.51
Flag leaf length (mm)	163.3	5.26	147.6	7.99	163.6	7.38	142.2	7.34	n/a	148.0	13.67	
Flag leaf width (mm)	17.3	0.57	15.9	0.42	17.3	0.57	15.1	0.89	n/a	16.7	1.42	
Flag leaf SLA (m/g)	0.0162	0.00023	0.0175	0.00020	0.0168	0.00123	0.0162	0.00076	n/a		0.0160	0.00012
Flag leaf area	2157	157.7	1760	186.1	2226	144.2	1327	50.1	n/a		1783	269.0
Early leaf counts	3.0	0	3.1	0.11	3.2	0.29	3.6	0.11	3.1		0.11	3.4
Early leaf length (mm)	94.2	4.04	104.7	2.88	103.8	1.86	98.1	1.40	74.5		4.69	93.4
Early leaf width (mm)	4.9	0.06	4.7	0.15	5.7	0.17	5.4	0.15	6.1	0.24	5.0	0.10
Early leaf angle (^{0})	44.9	n/a	52.1	n/a	35.9	n/a	41.8	n/a	29.8	n/a	42.1	n/a
50% emergence (DAS)	7.7	n/a	7.3	n/a	7.7	n/a	7.7	n/a	7.7	n/a	7.7	n/a
TGW (g)	41.5	n/a	32.6	n/a	34.8	n/a	33.8	n/a	33.2	n/a	38.9	n/a
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0084	n/a	0.0093	n/a	0.0085	n/a	0.0087	n/a	0.0078	n/a	0.0082	n/a
RGR_{GA} (cm^{-2} cm^{-2} d^{-1})	0.0101	n/a	0.0098	n/a	0.0090	n/a	0.0090	n/a	0.0083	n/a	0.0082	n/a
SLA (m/g)	0.0346	n/a	0.0312	n/a	0.0358	n/a	0.0313	n/a	0.0307	n/a	0.0325	n/a
LAR	116.4	n/a	119.7	n/a	138.6	n/a	122.5	n/a	130.0	n/a	125.0	n/a
LWR	0.362	n/a	0.393	n/a	0.402	n/a	0.404	n/a	0.437	n/a	0.395	n/a
NAR	0.794	n/a	0.879	n/a	0.730	n/a	0.739	n/a	0.757	n/a	0.774	n/a
ABGW (g)	0.0556	n/a	0.0679	n/a	0.0700	n/a	0.0681	n/a	0.0474	n/a	0.0683	n/a
RWR	0.253	n/a	0.290	n/a	0.260	n/a	0.234	n/a	0.230	n/a	0.294	n/a
Early green area (cm^2)	10.4	n/a	12.7	n/a	13.8	n/a	11.7	n/a	8.1	n/a	11.9	n/a

Table App. 9b - Mean traits values for cultivars in the sand-bed (high density) experiment 2013-14.

	Hereward		KWS Santiago		Oakley		Panorama		Robigus		Volume	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	704.0	36.46	725.8	45.20	694.2	16.24	751.8	20.21	646.1	26.83	754.3	40.76
Time of max. growth rate (ptt)	986	24.5	934	34.9	904	24.4	911	23.9	894	57.7	842	16.4
Maximum growth rate (mm/ptt)	1.00	0.179	1.04	0.022	0.97	0.048	1.12	0.124	0.91	0.081	2.21	0.071
Early height (mm)	107.6	0.80	89.4	5.53	85.6	7.97	95.4	7.09	90.7	5.93	101.2	12.04
Final stem count	1.9	0.11	1.3	0.19	1.9	0.22	2.1	0.11	1.8	0.44	3.6	0.11
Tillering rate (stems/ptt)	0.0267	0.00125	0.0343	0.00275	0.0206	0.00024	0.0218	0.00245	0.0239	0.00333	0.0391	0.00673
Maximum stem number	4.4	0.475	5.8	0.345	5.6	0.204	3.4	0.011	5.6	0.092	10.0	0.589
Time of max. stem number (ptt)	211.7	15.65	235.2	3.82	307.9	5.55	202.4	13.92	292.7	28.30	318.9	42.40
% stem loss	55.8	7.05	77.3	2.42	66.5	3.17	36.4	3.79	68.2	8.49	64.1	2.43
75% spike emergence (ptt)	871	5.5	903	11.5	856	30.8	877	15.3	873	13.9	785	11.7
Flag leaf angle (^{0})	21.1	1.54	25.6	6.95	23.7	3.37	16.9	3.27	21.8	2.80	68.2	8.74
Flag leaf length (mm)	166.1	4.27	169.8	3.03	188.5	18.43	172.1	8.52	173.1	6.01	93.5	7.34
Flag leaf width (mm)	17.9	0.51	16.6	0.06	18.2	0.88	17.3	0.71	18.8	0.66	12.7	0.91
Flag leaf SLA (m/g)	0.0168	0.00031	0.0182	0.00175	0.0179	0.00062	0.0167	0.00031	0.0181	0.00013	0.0214	0.00059
Flag leaf area (mm^2)	2333	126.4	2414	155.1	2576	508.9	2206	184.3	2520	288.0	822	124.8
Early leaf counts	3.7	0.19	3.2	0.11	3.2	0.11	2.9	0.11	3.0	0.00	3.9	0.22
Early leaf length (mm)	103.7	1.15	100.8	4.62	93.3	6.18	103.3	1.92	98.9	1.40	114.3	5.19
Early leaf width (mm)	5.2	0.15	4.8	0.22	4.6	0.24	5.2	0.10	4.8	0.15	9.4	0.34
Early leaf angle (^{0})	34.7	n/a	76.2	n/a	50.5	n/a	44.3	n/a	61.1	n/a	52.6	n/a
50% emergence (DAS)	7.7	n/a	7.7	n/a	7.7	n/a	7.3	n/a	7.7	n/a	7.7	n/a
TGW (g)	38.1	n/a	40.0	n/a	40.6	n/a	39.6	n/a	36.4	n/a	46.9	n/a
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0079	n/a	0.0082	n/a	0.0083	n/a	0.0088	n/a	0.0073	n/a	0.0086	n/a
RGR_{GA} (cm^{-2} cm^{-2} d^{-1})	0.0073	n/a	0.0085	n/a	0.0090	n/a	0.0096	n/a	0.0086	n/a		n/a
SLA	0.0284	n/a	0.0298	n/a	0.0308	n/a	0.0331	n/a	0.0330	n/a	0.0375	n/a
LAR	115.0	n/a	116.0	n/a	114.6	n/a	127.5	n/a	124.0	n/a	159.1	n/a
LWR	0.433	n/a	0.402	n/a	0.384	n/a	0.388	n/a	0.408	n/a	0.427	n/a
NAR	0.756	n/a	0.824	n/a	0.845	n/a	0.864	n/a	0.671	n/a	0.630	n/a
ABGW (g)	0.0693	n/a	0.0630	n/a	0.0638	n/a	0.0712	n/a	0.0486	n/a	0.1208	n/a
RWR	0.233	n/a	0.276	n/a	0.292	n/a	0.256	n/a	0.276	n/a	0.219	n/a
Early green area (cm^2)	10.2	n/a	10.3	n/a	11.3	n/a	13.0	n/a	9.3	n/a	22.6	n/a

Table App. 10a - Mean traits values for cultivars in the sand-bed (high density) experiment 2013-14.

	Claire		Conqueror		Duxford		Gallant		Gerald		Grafton	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	724.6	9.86	770.3	35.02	745.2	24.49	690.7	21.94	781.8	30.33	653.0	20.71
Time of maximum growth rate (ptt)	945	34.8	804	55.7	858	87.0	775	96.4	878	42.3	917	70.2
Maximum growth rate (mm ptt)	1.18	0.057	0.84	0.056	0.89	0.100	0.84	0.097	1.13	0.118	0.92	0.037
Early height (mm)	92.6	3.56	99.3	6.74	111.9	3.11	104.3	3.02	78.6	1.93	97.8	8.99
Final stem count	2.2	0.22	2.7	0.38	2.4	0.29	2.4	0.48	3.6	0.68	2.3	0.19
Rate of tillering (stem ptt)	0.0211	0.00197	0.0250	0.00410	0.0227	0.00123	0.0226	0.00203	0.0253	0.00187	0.0419	0.00132
Maxmimum stem number	5.8	0.09	5.9	0.26	4.1	0.40	4.8	0.53	9.2	0.54	7.9	0.62
Time of max. stem number (ptt)	319	14.9	297	23.2	218	18.4	247	5.7	413	3.8	257	17.7
% Stem loss	61.7	3.36	55.2	4.74	38.3	14.08	47.0	13.67	61.8	5.88	70.3	2.59
75% spike emergence (ptt)	880	7.8	869	26.0	824	31.7	807	39.6	923	22.7	822	24.4
Flag leaf angle (^{0})	33.3	3.26	20.3	4.94	18.5	1.16	30.3	3.77	14.3	0.52	21.8	0.31
Flag leaf length (mm)	151.9	3.00	171.2	2.00	174.6	3.87	157.4	2.87	n/a		157.9	2.98
Flag leaf width (mm)	16.6	0.29	17.4	0.59	18.2	0.51	16.6	0.46	n/a		17.3	0.65
Flag leaf SLA (m/g)	0.0201	0.00213	0.0180	0.00018	0.0167	0.00024	0.0168	0.00200	n/a		0.0167	0.00118
Flag leaf area (mm^2)	1806	188.9	2360	109.4	2331	255.0	1447	252.3	n/a		1936	70.0
Early leaf counts	2.9	0.11	3.1	0.11	3.8	0.22	3.3	0.19	3.0	0.00	3.1	0.11
Early leaf length (mm)	4.9	0.06	4.7	0.15	5.7	0.17	5.4	0.15	6.1	0.24	5.0	0.10
Early leaf width (mm)	5.0	0.10	4.6	0.11	5.6	0.05	5.0	0.19	5.8	0.10	5.2	0.24
Early leaf angle (^{0})	51.9	0.24	46.8	2.22	40.2	4.01	45.2	3.70	32.1	4.50	47.8	4.07
50% emergence (DAS)	8.3	0.33	7.3	0.33	7.3	0.33	7.3	0.33	8.3	0.33	7.0	0.00
TGW (g)	41.5	n/a	32.6	n/a	34.8	n/a	33.8	n/a	33.2	n/a	38.9	n/a
RGR_{DWT} (g-1 g-1 d-1)	0.0084	n/a	0.0093	n/a	0.0085	n/a	0.0087	n/a	0.0078	n/a	0.0082	n/a
RGR_{GA} (cm^{-2} cm^{-2} d^{-1})	0.0101	n/a	0.0098	n/a	0.0090	n/a	0.0090	n/a	0.0083	n/a	0.0082	n/a
SLA	0.0346	n/a	0.0312	n/a	0.0358	n/a	0.0313	n/a	0.0307	n/a	0.0325	n/a
LAR	116.4	n/a	119.7	n/a	138.6	n/a	122.5	n/a	130.0	n/a	125.0	n/a
LWR	0.362	n/a	0.393	n/a	0.402	n/a	0.404	n/a	0.437	n/a	0.395	n/a
NAR	0.79	n/a	0.88	n/a	0.73	n/a	0.74	n/a	0.76	n/a	0.77	n/a
ABGW (g)	0.056	n/a	0.068	n/a	0.070	n/a	0.068	n/a	0.047	n/a	0.068	n/a
RWR	0.253	n/a	0.290	n/a	0.260	n/a	0.234	n/a	0.230	n/a	0.294	n/a
Early green area (cm^2)	10.4	n/a	12.7	n/a	13.8	n/a	11.7	n/a	8.1	n/a	11.9	n/a

Table App. 10b - Mean traits values for cultivars in the sand-bed (high density) experiment 2013-14.

	Hereward		KWS Santiago		Oakley		Panorama		Robigus		Volume	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Final height (mm)	749.3	96.07	760.1	25.39	706.8	15.26	743.2	35.46	709.4	20.21	792.8	5.86
Time of maximum growth rate (ptt)	901	64.8	814	56.3	947	39.3	842	45.3	961	17.7	806	23.3
Maximum growth rate (mm ptt)	0.83	0.025	1.03	0.105	1.04	0.060	1.08	0.125	1.24	0.130	2.07	0.105
Early height (mm)	93.8	4.64	81.3	2.04	87.7	5.67	96.2	1.42	94.2	5.39	97.9	4.54
Final stem count	2.1	0.29	1.7	0.19	2.8	0.11	2.1	0.11	2.2	0.11	4.0	0.33
Rate of tillering (stem ptt)	0.0223	0.00131	0.0302	0.00454	0.0251	0.00471	0.0175	0.00376	0.0296	0.00242	0.0372	0.00228
Maxmimum stem number	5.7	0.34	6.5	0.22	6.9	0.30	4.9	0.21	7.5	0.63	12.7	0.75
Time of max. stem number (ptt)	292	27.7	277	17.9	340	46.5	323	48.1	318	40.8	394	21.5
% Stem loss	62.2	6.23	74.1	3.27	59.6	3.30	57.0	2.92	70.0	3.44	67.9	4.65
75% spike emergence (ptt)	867	10.7	891	14.5	876	26.7	866	20.7	874	10.3	788	14.5
Flag leaf angle (^{0})	17.2	2.08	25.0	7.24	34.3	7.06	22.9	6.33	18.6	1.97	63.3	4.85
Flag leaf length (mm)	182.3	0.52	190.4	7.21	195.1	5.44	185.5	20.32	181.5	5.26	101.0	3.35
Flag leaf width (mm)	18.9	0.51	18.5	0.41	18.4	0.43	18.0	0.93	18.3	0.16	13.3	0.29
Flag leaf SLA (m/g)	0.0174	0.00073	0.0173	0.00114	0.0190	0.00115	0.0171	0.00015	0.0205	0.00065	0.0216	0.00121
Flag leaf area (mm^2)	2294	380.8	2336	494.4	2746	184.5	2025	731.2	1858	402.5	970	84.2
Early leaf counts	3.0	0.33	3.1	0.11	3.0	0.19	3.1	0.11	3.0	0.00	3.8	0.11
Early leaf length (mm)	5.2	0.15	4.8	0.22	4.6	0.24	5.2	0.10	4.8	0.15	9.4	0.34
Early leaf width (mm)	4.9	0.15	4.6	0.11	4.9	0.11	5.3	0.22	4.6	0.15	9.3	0.25
Early leaf angle (^{0})	36.8	4.18	64.7	3.98	53.0	7.08	50.1	2.42	68.3	5.17	46.0	3.67
50% emergence (DAS)	7.3	0.33	8.0	0.00	7.0	0.00	7.3	0.33	7.0	0.00	7.3	0.33
TGW (g)	38.1	n/a	40.0	n/a	40.6	n/a	39.6	n/a	36.4	n/a	46.9	n/a
RGR_{DWT} (g^{-1} g^{-1} d^{-1})	0.0079	n/a	0.0082	n/a	0.0083	n/a	0.0088	n/a	0.0073	n/a	0.0086	n/a
RGR_{GA} (cm^{-2} cm^{-2} g^{-1})	0.0073	n/a	0.0085	n/a	0.0090	n/a	0.0096	n/a	0.0086	n/a		n/a
SLA	0.0284	n/a	0.0298	n/a	0.0308	n/a	0.0331	n/a	0.0330	n/a	0.0375	n/a
LAR	115.0	n/a	116.0	n/a	114.6	n/a	127.5	n/a	124.0	n/a	159.1	n/a
LWR	0.433	n/a	0.402	n/a	0.384	n/a	0.388	n/a	0.408	n/a	0.427	n/a
NAR	0.76	n/a	0.82	n/a	0.84	n/a	0.86	n/a	0.67	n/a	0.63	n/a
ABGW (g)	0.069	n/a	0.063	n/a	0.064	n/a	0.071	n/a	0.049	n/a	0.121	n/a
RWR	0.233	n/a	0.276	n/a	0.292	n/a	0.256	n/a	0.276	n/a	0.219	n/a
Early green area (cm^2)	10.2	n/a	10.3	n/a	11.3	n/a	13.0	n/a	9.3	n/a	22.6	n/a

Table App. 11a - Mean cultivar trait values in the field experiment 2012-13.

	Claire		Conqueror		Duxford		Gallant		Grafton	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Ear index	37.2	1.56	41.8	1.40	29.9	1.18	34.7	7.59	37.0	1.63
Flag leaf length (mm)	184.0	5.71	172.4	14.37	191.7	4.20	169.0	9.73	167.2	6.61
Flag leaf width (mm)	14.9	0.033	15.8	0.122	17.8	0.406	15.1	0.346	15.8	0.721
Flag leaf area (mm^2)	2163	170.5	2249	307.2	2921	35.5	2028	136.7	2003	124.1
Flag leaf SLA (m/g)	0.0260	0.00208	0.0265	0.00087	0.0312	0.00070	0.0259	0.00083	0.0238	0.00133
Flag leaf angle (^{0})	24.1	1.26	31.4	1.24	23.5	1.97	34.9	1.97	31.7	3.54
Early leaf number	4.5	0.20	5.9	1.09	4.6	0.12	5.5	0.34	5.8	0.21
Early height (mm)	72.8	6.89	75.1	2.82	0.0	4.50	78.4	7.00	70.3	5.14
Final height (mm)	711.9	24.14	705.3	33.97	780.7	11.71	682.1	15.61	668.9	5.24
Time of max. growth rate (ptt)	615	263.0	813	39.1	925	37.0	912	8.8	876	29.9
Final stem count	1.6	0.17	1.7	0.09	1.9	0.26	1.6	0.07	2.1	0.33
% Stem loss	44.5	3.14	32.8	6.50	28.8	6.68	31.4	5.23	38.1	6.74
Time of max. stem no. (ptt)	738	93.3	284	59.2	904		285	29.2	625	211.8
Max stem number	3.0	0.42	2.5	0.30	2.7	0.62	2.4	0.14	3.3	0.40
Rate of tillering (stem/ptt)	0.0033	0.00124	0.0157	0.00861	0.0090	0.00683	0.0106	0.00185	0.0078	0.00442
Early leaf area (mm^2)	9.8	1.48	7.2	0.17	6.9	0.25	6.2	0.53	5.8	0.82
Early green area (mm^2)	10.7	1.71	7.8	0.28	7.6	0.15	6.7	0.51	6.4	0.87
ABGW (g)	0.064	0.0090	0.047	0.0020	0.048	0.0018	0.044	0.0003	0.044	0.0046
Early SLA (m/g)	0.0276	0.00094	0.0270	0.00046	0.0270	0.00104	0.0245	0.00168	0.0249	0.00052
TGW (g)	50.1		41.5		35.8		40.0		41.2	

Table App. 11b - Mean cultivar trait values for the field experiment 2012-13.

	Hereward		KWS Santiago		Oakley		Panorama		Robigus	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Ear index	32.3	3.06	32.4	8.80	35.1	1.03	32.3	1.62	35.6	1.36
Flag leaf length (mm)	172.4	6.71	199.3	4.74	190.1	4.87	202.7	5.76	196.0	5.88
Flag leaf width (mm)	16.6	0.296	16.4	0.058	16.1	0.219	15.5	0.723	17.3	0.198
Flag leaf area (mm^2)	2358	35.2	2857	65.6	2668	142.2	2311	133.4	2888	333.6
Flag leaf SLA (m/g)	0.0268	0.00237	0.0248	0.00050	0.0285	0.00067	0.0268	0.00137	0.0286	0.00080
Flag leaf angle (^{0})	27.1	2.54	32.8	0.98	26.3	0.41	32.2	4.89	33.6	1.67
Early leaf number	4.8	0.38	6.0	0.75	4.7	0.19	5.8	0.47	5.9	0.40
Early height (mm)	72.4	4.23	73.0	1.63	82.9	3.07	85.6	3.74	77.7	5.33
Final height (mm)	731.3	19.90	779.6	18.17	711.1	24.12	757.9	21.58	725.5	8.18
Time of max. growth rate (ptt)	828	54.4	864	17.2	863	25.7	883	47.6	896	21.2
Final stem count	1.7	0.26	1.9	0.23	1.9	0.20	2.3	0.29	2.2	0.26
% Stem loss	29.4	15.98	30.8		31.4	4.15	31.1	2.99	25.9	14.32
Time of max. stem no. (ptt)	483	192.7	404		662		739	116.3	522	191.8
Max stem number	2.3	0.01	3.3		2.8	0.20	3.4	0.41	3.0	0.23
Rate of tillering (stem/ptt)	0.0071	0.00450	0.0086		0.0016	0.00087	0.0028	0.00088	0.0089	0.00474
Early leaf area (mm^2)	5.5	0.60	5.5	1.51	7.5	0.87	7.2	0.64	6.1	0.30
Early green area (mm^2)	6.1	0.58	6.1	1.63	8.1	0.93	7.7	0.71	6.6	0.31
ABGW (g)	0.043	0.0028	0.042	0.0077	0.047	0.0064	0.055	0.0086	0.054	0.0027
Early SLA (m/g)	0.0243	0.00026	0.0231	0.00216	0.0274	0.00070	0.0250	0.00091	0.0277	0.00073
TGW (g)	41.4		38.2		47.0		42.7		40.4	

Table 12a - Mean trait values for cultivars in the field experiment 2013-14 (early drilled treatment).

	Claire		Conqueror		Duxford		Gallant		Grafton	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Ear index	36.1	2.91	38.1	5.77	34.3	4.19	39.4	2.53	35.6	4.56
Flag leaf length (mm)	186.4	2.88	184.4	6.72	197.5	11.36	184.1	10.85	186.1	5.46
Flag leaf width (mm)	17.4	0.45	17.5	0.64	17.9	0.35	17.5	0.87	17.9	0.27
Flag leaf area (mm^2)	2493	41.1	2464	224.9	2916	283.4	2509	250.0	2531	58.0
Flag leaf SLA (m/g)	0.024	0.00071	0.023	0.00075	0.025	0.00091	0.023	0.00087	0.024	0.00060
Flag leaf angle (^{0})	20.6	3.13	18.6	1.87	18.4	3.23	20.2	0.66	16.4	3.41
Early leaf number	10.9	1.11	9.5	0.63	8.9	0.84	9.2	0.29	11.7	0.70
Early height (mm)	97.2	4.59	111.3	4.20	120.3	5.26	121.1	3.53	99.7	6.47
Final height (mm)	907	12.1	916	9.9	991	15.3	887	16.5	816	7.1
Time of max. growth rate (ptt)	1104	33.6	1020	68.5	1088	6.6	1060	46.2	1066	46.0
Final stem count	2.5		2.9	0.088	2.5	0.208	2.7	0.067	2.6	0.033
% Stem loss	43.8	2.25	31.0	3.42	34.4	4.11	19.8	1.59	41.2	1.54
Time of max. stem no. (ptt)	334	8.0	399	67.1	341	18	335	14.3	312	9.7
Max stem number	4.5	0.18	4.2	0.30	3.8	0.11	3.4	0.13	4.4	0.06
Rate of tillering (stem/ptt)	0.018	0.0015	0.014	0.0045	0.014	0.0012	0.013	0.0019	0.020	0.0007
Early leaf area (mm)	24.3	2.00	24.3	3.97	18.8	3.37	23.3	2.41	17.8	0.76
Early green area (mm^2)	25.7	2.12	26.3	4.63	19.8	3.49	25.6	2.83	19.4	0.99
ABGW (g)	0.165	0.013	0.141	0.017	0.122	0.018	0.146	0.019	0.129	0.007
Early SLA (m/g)	0.026	0.00058	0.029	0.00084	0.029	0.00042	0.028	0.00117	0.026	0.00080
TGW (g)	41.5		32.6		34.8		33.8		38.9	
Weed-free yield (kg m^2)	1.26	0.112	1.37	0.171	1.30	0.033	1.25	0.376	1.32	0.144

Table 12b - Mean trait values for cultivars in the field experiment 2013-14 (early drilled treatment).

	Hereward		KWS Santiago		Oakley		Panorama		Robigus	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Ear index	43.7	11.50	30.3	1.34	41.6	4.42	33.0	5.62	37.2	1.48
Flag leaf length (mm)	194.7	15.29	203.6	11.79	177.2	4.37	210.8	10.21	194.5	4.99
Flag leaf width (mm)	19.4	1.21	17.8	0.70	16.9	0.38	17.7	0.61	18.5	0.27
Flag leaf area (mm^2)	3001	425.6	2838	276.8	2309	98.2	2862	321.7	2764	123.2
Flag leaf SLA (m/g)	0.024	0.00123	0.023	0.00006	0.024	0.00084	0.023	0.00049	0.025	0.00042
Flag leaf angle (^{0})	13.2	2.16	15.1	0.70	15.9	3.12	15.1	1.26	16.5	1.16
Early leaf number	10.3	0.61	10.6	1.54	8.6	1.16	9.9	1.75	9.3	0.82
Early height (mm)	110.2	6.11	95.8	0.70	99.8	5.88	115.3	2.10	102.6	4.68
Final height (mm)	913	15.4	1006	16.2	842	21.7	935	18.9	865	12.4
Time of max. slope (ptt)	1032	41.3	1045	43.8	1022	33.0	1031	49.2	1123	59.9
Final stem count	2.7	0.203	2.3	0.273	2.3	0.058	2.4	0.115	2.4	0.067
% Stem loss	29.0	2.19	46.6	3.02	46.0	1.25	38.4	4.57	41.1	0.66
Time of max. stem no. (ptt)	353	25.1	348	17.4	443	65.8	486	58.6	341	13.6
Max stem number	3.9	0.29	4.4	0.48	4.3	0.20	3.9	0.21	4.1	0.07
Rate of tillering (stem/ptt)	0.014	0.0018	0.016	0.0013	0.012	0.0034	0.008	0.0012	0.016	0.0015
Early leaf area (mm^2)	16.9	1.41	18.3	3.22	16.0	2.45	21.1	3.94	22.3	1.55
Early green area (mm^2)	17.9	1.46	20.0	3.89	16.9	2.46	23.3	4.63	24.1	1.44
ABGW (g)	0.129	0.0079	0.135	0.0274	0.108	0.0148	0.146	0.0303	0.139	0.0105
Early SLA (m/g)	0.023	0.00032	0.024	0.00017	0.026	0.00006	0.029	0.00078	0.028	0.00008
TGW (g)	38.1		40.0		40.6		39.6		36.4	
Weed-free yield (kg m^2)	1.05	0.548	1.40	0.446	1.22	0.284	1.25	0.186	1.17	0.053

Table App. 13a - Mean trait values for cultivars in the field experiment 2013-14 (late drilled treatment).

	Claire		Conqueror		Duxford		Gallant		Grafton	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Ear index	54.1	5.08	54.3	3.18	51.9	4.27	54.0	3.66	59.7	0.12
Flag leaf length (mm)	190.1	2.38	179.7	1.51	202.9	9.20	183.3	7.23	195.5	6.24
Flag leaf width (mm)	16.8	0.145	17.5	0.067	17.9	0.924	17.6	0.481	17.8	0.606
Flag leaf area (mm^2)	2382	85.9	2267	137.0	2625	349.0	2233	129.6	2391	192.1
Flag leaf SLA (m/g)	0.026	0.00084	0.022	0.00094	0.025	0.00058	0.024	0.00023	0.026	0.00145
Flag leaf angle (^{0})	18.4	1.32	15.0	1.48	13.8	1.39	27.4	4.58	16.0	2.66
Early leaf number	6.5	0.033	6.0	0.633	5.3	0.984	4.8	0.438	6.5	0.463
Early height (mm)	89.5	1.74	87.4	3.84	95.5	2.19	85.0	2.72	83.3	2.54
Final height (mm)	906	2.9	901	13.7	973	16.2	867	0.1	830	13.4
Time of max. slope (ptt)	779	3.2	742	29.0	767	2.9	740	27.2	771	22.8
Final stem count	3.3	0.12	2.6	0.25	3.0	0.18	2.6	0.17	3.2	0.44
% Stem loss	2.9		22.2	11.08	34.8		4.7	12.91	-3.3	25.57
Time of max. stem no. (ptt)	376		490	128.4	862		520	160.1	420	46.4
Max stem number	3.2		3.4	0.181	4.1		3.0	0.655	3.2	0.338
Rate of tillering (stem/ptt)	0.0080		0.0069	0.00139	0.0038		0.0050	0.00038	0.0069	0.00036
Early leaf area (mm^2)	12.6	0.56	13.0	1.17	9.5	1.36	10.2	0.74	11.5	1.08
Early green area (mm^2)	13.6	0.52	13.8	1.21	10.5	1.58	11.0	0.67	12.5	1.30
ABGW (g)	0.109	0.0052	0.088	0.0066	0.081	0.0122	0.077	0.0077	0.091	0.0072
Early SLA (m/g)	0.0234	0.00062	0.0263	0.00087	0.0235	0.00086	0.0247	0.00091	0.0247	0.00016
TGW (g)	41.5		32.6		34.8		33.8		38.9	
Weed-free yield (kg m^2)	1.32	0.023	1.44	0.009	1.34	0.016	1.29	0.022	1.33	0.013

Table App. 13b - Mean trait values for cultivars in the field experiment 2013-14 (late drilled treatment).

	Hereward		KWS Santiago		Oakley		Panorama		Robigus	
Cultivar traits	Mean	±	Mean	±	Mean	±	Mean	±	Mean	±
Ear index	55.0	4.01	49.5	3.77	53.7	3.94	51.3	2.70	43.2	1.73
Flag leaf length (mm)	205.5	9.99	211.4	12.80	192.4	7.35	202.7	6.43	200.7	6.30
Flag leaf width (mm)	19.1	0.338	17.9	0.624	18.2	0.408	17.8	0.458	18.2	0.636
flag leaf area (mm^2)	3078	215.6	2863	204.3	2601	140.6	2518	133.6	2830	176.1
Flag leaf SLA (m/g)	0.027	0.00094	0.025	0.00007	0.026	0.00019	0.024	0.00058	0.026	0.00065
Flag leaf angle (^{0})	11.1	0.84	13.6	1.07	15.2	1.21	15.7	2.32	13.3	0.96
Early leaf number	4.6	0.233	5.3	0.296	5.6	0.163	6.3	0.357	5.4	0.133
Early height (mm)	85.0	4.16	87.7	4.72	80.9	2.07	96.9	3.41	92.0	1.35
Final height (mm)	907	11.1	1000	8.3	894	13.1	931	21.1	859	9.7
Time of max. slope (ptt)	770	24.7	790	37.3	801	26.0	778	36.2	760	8.0
Final stem count	3.2	0.35	3.2	0.18	3.0	0.15	3.0	0.22	3.5	0.26
% Stem loss	-8.4	17.10	13.5	3.35	-0.5	4.46	10.1	6.40	-4.0	8.44
Time of max. stem no. (ptt)	467	37.6	441	66.9	358	16.6	413	63.6	476	143.4
Max stem number	3.0	0.175	3.5	0.049	3.0	0.074	3.3	0.104	3.4	0.095
Rate of tillering (stem/ptt)	0.0056	0.00015	0.0074	0.00120	0.0078	0.00070	0.0075	0.00140	0.0078	0.00344
Early leaf area (mm^2)	8.8	0.49	10.5	0.72	10.7	1.38	10.7	1.06	9.1	2.45
Early green area (mm^2)	9.3	0.55	11.1	0.60	11.6	1.77	11.5	0.99	9.8	2.15
ABGW (g)	0.072	0.0036	0.079	0.0038	0.078	0.0149	0.087	0.0045	0.078	0.0044
Early SLA (m/g)	0.0242	0.00052	0.0256	0.00066	0.0248	0.00039	0.0255	0.00035	0.0265	0.00121
TGW (g)	38.1		40.0		40.6		39.6		36.4	
Weed-free yield (kg m^2)	1.13	0.078	1.39	0.090	1.23	0.030	1.30	0.009	1.17	0.012

Table App. 14a - Pearson's correlations coefficients of traits in the 2011-12 sand-beds experiment. * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-							
50% emergence	2	0.0168	-						
ABGW	3	0.2075	-0.1428	-					
Early green area	4	0.0905	-0.1674	**0.9533*** **	-				
Early height	5	0.249	-0.1015	**0.3376***	**0.38***	-			
Early leaf counts	6	**0.3839***	-0.1451	0.295	0.2354	0.1475	-		
Final height	7	-0.1674	0.2034	0.1895	0.1881	0.1884	0.1366	-	
Flag leaf length	8	0.1467	0.0121	-0.1105	-0.0902	**0.3703***	0.1496	0.2698	-
Flag leaf width	9	-0.1264	0.2042	-0.1775	-0.0547	-0.0174	-0.0762	0.0303	**0.4419****
Maximum stem number	10	0.2512	-0.1373	-0.0311	-0.0862	-0.235	**0.5322*****	-0.2726	-0.1841
LAR	11	-0.1401	-0.1165	0.2526	**0.3474***	**0.5102*****	-0.037	0.1951	0.3025
LWR	12	**-0.4539****	-0.0363	**-0.4907****	**-0.4544****	0.0403	-0.1705	**0.3274***	0.2726
Maximum growth rate	13	**0.3241***	-0.1387	0.1645	0.0977	-0.0653	0.3009	0.207	0.0572
NAR	14	**0.4387****	-0.1394	-0.0406	-0.0573	**0.4643****	0.0352	**-0.3451***	0.1234
RGR_{DWT}	15	**0.4584****	-0.1746	0.2835	0.2121	**0.5686*****	0.141	-0.0434	0.2289
RGR_{GA}	16	**0.357***	-0.0958	0.0096	-0.006	**0.5092*****	-0.0665	-0.1317	0.1263
RWR	17	**-0.3453***	-0.0292	**-0.5035****	**-0.4093****	-0.2244	-0.0978	-0.0286	0.1372
Early SLA	18	0.1967	0.0201	**0.6366*****	**0.6892*****	0.2955	0.0703	-0.0062	0.0376
Rate of tillering	19	0.0977	-0.1763	-0.0155	-0.0689	**-0.3195***	**0.3799***	0.0225	-0.041
Time of max. growth rate	20	0.111	0.1788	-0.0073	0.0081	-0.1657	0.093	0.0907	-0.2677
Time of max. stem number	21	0.1055	0.0871	-0.0631	-0.0891	-0.1042	0.1202	-0.2441	-0.2196
Seed return ($plant^{-1}$)	22	-0.0082	0.0095	**-0.3722***	**-0.4417****	**-0.5362*****	-0.0276	-0.1885	**-0.3997***

Table App. 14b - Pearson's correlations coefficients of traits in the 2011-12 sand-beds experiment. * = P<0.05; **=P<0.01; ***=P<0.001

Flag leaf width	9	-							
Maximum stem number	10	-0.1524	-						
LAR	11	0.2716	**-0.5192*** **	-					
LWR	12	0.0773	-0.2039	0.0424	-				
Maximum growth rate	13	-0.0852	0.1245	0.2936	-0.2721	-			
NAR	14	0.1876	-0.1894	**0.3571***	-0.1441	-0.0258	-		
RGR_{DWT}	15	-0.046	-0.2976	**0.5403*** **	0.0307	0.1179	**0.7753*** **	-	
RGR_{GA}	16	0.1857	**-0.3213***	**0.3348***	0.0811	-0.0624	**0.8905*** **	**0.7925*** **	-
RWR	17	0.0501	0.2801	**-0.5129*** **	**0.4432****	**-0.4816****	**-0.3214***	**-0.4767****	-0.2821
Early SLA	18	0.0815	-0.2792	**0.618*** **	**-0.6849*** **	0.3002	0.1467	0.2603	-0.0082
Rate of tillering	19	-0.1573	0.2236	**-0.3186***	-0.0155	0.0486	-0.2118	-0.1299	-0.1794
Time of max. growth rate	20	-0.1364	0.0555	-0.0823	-0.0171	0.3037	-0.1664	-0.1188	-0.2171
Time of max. stem number	21	-0.0842	**0.7413*** **	**-0.3637***	-0.1863	0.0449	-0.1183	-0.2846	-0.2366
Seed return ($plant^{-1}$)	22	-0.2077	**0.3301***	**-0.3555***	0.1448	0.2135	-0.1469	-0.1589	-0.1219
		9	10	11	12	13	14	15	16

RWR	17	-				
Early SLA	18	**-0.66*** **	-			
Rate of tillering	19	0.2245	-0.1845	-		
Time of max. growth rate	20	-0.1363	0.0224	0.0049	-	
Time of max. stem number	21	0.1606	-0.181	**-0.4395****	0.0349	-
Seed return ($plant^{-1}$)	22	0.1244	**-0.4518****	0.1005	0.0113	0.2794
		17	18	19	20	21

Table App. 15a - Pearson's correlations coefficients of traits in the 2012-13 sand-beds experiment (*A. myosuroides* treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-						
50% emergence	2	-0.0602	-					
Spike emergence	3	0.1829	0.0721	-				
% stem loss	4	0.0644	0.0363	-0.3804	-			
ABGW	5	0.0658	-0.1044	0.4009	**-0.5588****	-		
Early green area	6	-0.0903	-0.0608	-0.0884	-0.2858	**0.7265*****	-	
Early height	7	-0.3217	-0.1056	-0.3429	0.0199	0.1362	**0.5577****	-
Early leaf angle	8	0.0009	-0.3768	0.2109	0.1158	-0.1539	-0.3949	-0.2707
Early leaf counts	9	0.101	-0.0876	**0.4517***	-0.1591	0.2261	-0.0802	-0.2706
Early leaf length	10	-0.167	0.0801	0.0454	-0.1456	0.0916	0.2857	**0.4826***
Early leaf width	11	-0.1541	0.1058	-0.2294	0.2139	0.1183	**0.4646***	**0.5602****
Final height	12	-0.2079	-0.3913	-0.1813	0.3527	-0.0118	0.1733	**0.4275***
Final stem count	13	-0.1268	0.1015	0.241	**-0.7376*****	0.3657	0.229	0.0662
Flag leaf angle	14	0.2409	0.3953	-0.2011	0.059	-0.1231	-0.0593	0.0247
Flag leaf area	15	-0.0257	-0.1786	0.0997	0.046	-0.232	-0.2845	-0.0355
Flag leaf length	16	0.0092	-0.1427	0.1668	0.0778	-0.3187	-0.4108	-0.0832
Flag leaf width	17	0.2051	-0.1786	0.258	-0.1818	0.3535	0.0321	-0.2217
Maximum stem number	18	-0.1519	0.2339	-0.1441	0.1874	-0.184	-0.0315	0.1112
LAR	19	-0.3613	**-0.4487***	-0.1393	**-0.1879***	0.2878	**0.5956****	**0.6389****
LWR	20	**-0.519***	-0.1596	0.1723	**-0.4663***	**0.5758****	**0.4584***	0.3878
Maximum growth rate	21	0.1858	-0.3027	-0.2169	0.4555	-0.1309	-0.1415	0.0289
NAR	22	**0.4728***	0.2435	0.3849	-0.1778	0.3172	-0.095	-0.2078
RGR_{DWT}	23	0.2674	0.0641	0.1063	-0.1185	**0.6887*****	**0.5486****	0.1607
RGR_{GA}	24	0.1075	0.2711	-0.3832	0.2265	-0.0714	0.2432	**0.4488***
RWR	25	0.2831	0.011	-0.2281	**0.5606****	**-0.8549*****	**-0.6454*****	-0.2787
Early SLA	26	0.3448	-0.2708	-0.1956	0.2283	0.1	**0.468***	0.2031
Rate of tillering	27	-0.2163	-0.3206	0.1626	-0.1102	0.0821	-0.1576	-0.109
Time of maximum growth rate	28	0.0783	-0.043	0.1379	0.2061	0.2463	0.1331	0.1085
Time of maximum stem number	29	-0.0136	0.3088	-0.2974	0.0494	-0.2165	0.053	0.1009
Weed biomass ($plant^{-1}$)	30	-0.0484	0.1854	-0.2053	**0.5239***	-0.1781	-0.2801	0.0172
Seed return ($plant^{-1}$)	31	-0.0611	0.1455	-0.1012	0.3236	-0.2274	-0.3571	-0.1038
		1	2	3	4	5	6	7

Table App. 15b - Pearson's correlations coefficients of traits in the 2012-13 sand-beds experiment (*A. myosuroides* treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Early leaf angle	8	-						
Early leaf counts	9	**0.5861****	-					
Early leaf length	10	-0.0267	0.3084	-				
Early leaf width	11	-0.0835	0.1828	**0.6619*****	-			
Final height	12	0.1667	-0.0468	-0.0255	0.3096	-		
Final stem count	13	0.0983	0.4096	0.2025	-0.0242	-0.088	-	
Flag leaf angle	14	-0.0512	-0.1593	0.0554	0.1792	-0.0238	0.041	-
Flag leaf area	15	0.0838	-0.3639	-0.2733	-0.258	0.113	-0.2672	-0.26
Flag leaf length	16	0.1221	-0.2719	-0.1777	-0.2638	0.0662	-0.3013	-0.2112
Flag leaf width	17	0.0225	-0.0115	-0.1386	-0.067	-0.1529	-0.1876	-0.1482
Maximum stem number	18	0.318	**0.4315***	0.1462	0.2781	0.2312	**0.5062***	0.1281
LAR	19	-0.3884	-0.3501	0.2436	0.2503	0.2555	-0.063	-0.4124
LWR	20	-0.241	0.0803	0.4088	0.1788	0.0135	0.276	-0.3839
Maximum growth rate	21	0.0204	**-0.4248***	**-0.5516****	-0.2243	**0.6181****	**-0.4386***	0.0221
NAR	22	-0.0277	0.1073	0.0626	-0.1528	-0.34	0.1037	0.2163
RGR_{DWT}	23	-0.1135	0.1848	0.1794	0.3077	0.186	0.0612	0.0986
RGR_{GA}	24	-0.3974	**-0.4532***	0.3014	0.3159	0.09	-0.2215	0.3754
RWR	25	0.2444	-0.1763	-0.2967	-0.2035	0.0055	-0.385	0.1165
Early SLA	26	-0.0656	-0.1504	-0.1519	0.2241	0.3566	-0.2218	-0.04
Rate of tillering	27	0.4356*	0.3508	0.1764	0.123	0.2134	-0.0286	-0.162
Time of maximum growth rate	28	-0.1849	-0.3529	-0.2192	-0.0802	0.3117	-0.3396	-0.0907
Time of maximum stem number	29	-0.2137	-0.2852	-0.2665	-0.1591	-0.0824	0.349	0.2091
Weed biomass ($plant^{-1}$)	30	0.1922	0.0278	-0.042	0.1755	0.3124	-0.3899	0.2923
Seed return ($plant^{-1}$)	31	0.4072	0.2092	0.1484	0.1578	0.0855	-0.2404	0.3958
		8	9	10	11	12	13	14

Table App. 15c - Pearson's correlations coefficients of traits in the 2012-13 sand-beds experiment (*A. myosuroides* treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Flag leaf area	15	-						
Flag leaf length	16	**0.9532*** **	-					
Flag leaf width	17	0.503*	**0.464***	-				
Maximum stem number	18	-0.4017	-0.4031	**-0.464***	-			
LAR	19	0.2205	0.1183	0.0606	-0.3701	-		
LWR	20	-0.0451	-0.0709	0.1452	-0.1971	**0.6051****	-	
Maximum growth rate	21	0.3198	0.2801	-0.016	-0.167	-0.0185	-0.241	-
NAR	22	-0.0658	-0.0204	0.2235	-0.0999	-0.4044	0.1204	0.0771
RGR_{DWT}	23	-0.2207	-0.2416	0.2195	-0.0877	-0.0188	0.3204	0.2302
RGR_{GA}	24	-0.063	-0.0595	-0.2488	-0.077	0.0825	0.082	0.2908
RWR	25	0.2683	0.3127	-0.2004	0.1543	-0.3737	**-0.8589*****	0.2074
Early SLA	26	0.0283	-0.0706	-0.0021	-0.0517	0.2797	**-0.4228***	0.2432
Rate of tillering	27	-0.0425	0.0248	0.2273	-0.075	-0.129	0.1472	0.049
Time of maximum growth rate	28	0.2426	0.2191	0.1287	-0.3036	0.1131	0.2051	**0.7044*****
Time of maximum stem number	29	-0.1049	-0.1996	**-0.4736***	**0.4999***	-0.0562	-0.2279	-0.0159
Weed biomass ($plant^{-1}$)	30	-0.1981	-0.1296	-0.2023	0.1014	-0.4052	-0.2302	0.4001
Seed return ($plant^{-1}$)	31	-0.2403	-0.1154	-0.2183	0.096	**-0.4804***	-0.2774	0.0928
		15	16	17	18	19	20	21

Table App. 15d - Pearson's correlations coefficients of traits in the 2012-13 sand-beds experiment (*A. myosuroides* treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Maximum growth rate	21	**0.5083***	-						
NAR	22	0.4165*	**0.4373***	-					
RGR_{DWT}	23	-0.2763	**-0.6407*****	-0.1034	-				
RGR_{GA}	24	**-0.4545***	0.1133	-0.0487	0.2635	-			
RWR	25	0.0061	0.1694	-0.1812	-0.1395	-0.1547	-		
Early SLA	26	**0.4359***	**0.5311****	**0.479***	-0.2389	-0.0105	0.1092	-	
Rate of tillering	27	-0.0906	-0.318	0.1131	0.2226	0.0332	**-0.7918*****	-0.1761	-
Time of maximum growth rate	28	0.0573	0.2114	0.1468	0.1066	-0.083	0.2691	0.2306	-0.2492
Time of maximum stem number	29	0.0275	0.0581	0.0172	0.1664	-0.141	0.4012	-0.0093	-0.3387
Weed biomass ($plant^{-1}$)	30	22	23	24	25	26	27	28	29

Table App. 16a - Pearson's correlations coefficients of traits in the 2012-13 sand-beds experiment (*S. media* treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-							
50% Emergence	2	-0.1235	-						
75% spike emergence	3	0.1753	0.0632	-					
ABGW	4	0.1527	-0.1871	0.2378	-				
Early green area	5	0.213	-0.0806	0.1195	**0.7593*** **	-			
Early height	6	0.1628	0.0271	0.1874	0.3079	**0.5429** **	-		
Early leaf angle	7	-0.2442	**-0.4146***	0.0077	0.0920	-0.2594	-0.0489	-	
Early leaf counts	8	0.1523	-0.234	0.0403	0.0495	-0.0085	-0.0815	0.3204	-
Early leaf length	9	-0.0662	-0.0714	0.1387	0.1962	0.2819	**0.4445***	0.1873	**0.6537*** **
Early leaf width	10	0.1672	0.0495	0.0103	0.2621	**0.5192** **	**0.7224*** **	0.1038	0.3491
Final height	11	-0.113	-0.2659	0.1999	0.2225	0.1826	0.3548	-0.0714	-0.3013
Flag leaf SLA	12	0.0865	-0.0007	0.1088	0.3072	**0.4929** **	0.1331	-0.2441	0.2844
Flag leaf angle	13	0.3699	0.0151	0.0544	-0.1386	-0.0411	0.2618	0.0038	0.084
Flag leaf area	14	0.02	-0.0183	0.0876	0.1436	-0.1203	0.0687	0.1315	0.1031
Flag leaf length	15	0.0381	-0.0664	-0.005	-0.2937	**-0.4223** **	0.07	0.0439	-0.0389
Flag leaf width	16	0.3268	0.211	0.1768	-0.0816	-0.2413	0.1283	0.1937	-0.0927
LAR	17	-0.1016	-0.3153	-0.0652	0.3366	**0.4603** **	**0.6779*** **	0.1603	-0.1204
LWR	18	**-0.4418***	-0.1303	0.0418	**0.5989** **	0.3629	**0.4783***	**0.3641***	-0.0943
NAR	19	0.3625	0.241	**0.4244***	**0.5046***	0.1272	0.1626	-0.0708	-0.198
RGR_{DWT}	20	0.3417	-0.0355	0.3342	0.7334	**0.6545*** **	0.3641	-0.3227	-0.015
RGR_{GA}	21	0.2843	0.3095	0.2273	-0.1036	0.2184	**0.5801** **	**-0.6303*** **	-0.3868
RWR	22	0.2075	0.1297	-0.1574	**-0.8694** **	**-0.6102** **	**-0.408***	-0.2109	0.0065
Early SLA	23	**0.584** **	-0.2175	-0.0101	0.066	**0.481***	0.1313	**-0.4443***	0.1139
Time of maximum growth rate	24	0.1304	-0.2375	-0.0776	0.1189	0.0768	0.1322	-0.0027	0.0053
Weed biomass ($plant^{-1}$)	25	-0.1789	0.2032	0.048	0.2861	0.017	-0.0595	0.0756	0.1702
		1	2	3	4	5	6	7	8

Table App. 16b - Pearson's correlations coefficients of traits in the 2012-13 sand-beds experiment (S. media treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Early leaf counts	8	-							
Early leaf length	9	**0.7642*** **	-						
Early leaf width	10	0.1224	0.1199	-					
Final height	11	**0.4804***	0.3662	-0.0908	-				
Flag leaf SLA	12	0.0314	0.1533	-0.0509	-0.0929	-			
Flag leaf angle	13	0.2432	0.048	0.2722	0.3986	0.2885	-		
Flag leaf area	14	0.0904	-0.0605	**0.4616***	-0.0581	0.3866	**0.7345*** **	-	
Flag leaf length	15	0.0489	0.125	0.0968	-0.1631	0.2677	0.3765	0.3877	-
Flag leaf width	16	**0.4194***	**0.6098****	**0.6357*** **	0.1805	0.0671	0.2416	0.2902	0.0878
LAR	17	0.338	0.3135	**0.4222***	0.0358	-0.2079	0.2365	0.0196	-0.023
LWR	18	-0.0757	-0.0631	0.0252	0.0311	0.0854	0.3122	0.0049	**0.4837***
NAR	19	0.0019	0.1235	0.1695	0.0932	0.072	-0.0694	-0.3443	-0.2364
RGR_{DWT}	20	0.0375	0.2438	0.2944	0.0614	0.3226	0.0134	0.1521	0.1977
RGR_{GA}	21	-0.2646	-0.2592	-0.2941	-0.1442	0.2223	-0.1323	0.2382	0.1587
RWR	22	0.018	0.2623	0.0671	0.3076	0.2316	-0.2072	-0.1097	-0.2
Early SLA	23	-0.035	0.1691	0.2866	-0.3758	0.0555	-0.2886	-0.1604	-0.1327
Time of maximum growth rate	24	0.1506	0.0121	-0.037	0.3456	-0.0437	0.455*	0.152	-0.2773
		9	10	11	12	13	14	15	16

Table App. 16c - Pearson's correlations coefficients of traits in the 2012-13 sand-beds experiment (*S. media* treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

LAR	17	-							
LWR	18	**0.638*** **	-						
NAR	19	-0.0827	0.2833	-					
RGR_{DWT}	20	0.0268	0.2894	**0.5032***	-				
RGR_{DWT}	20	0.2594	-0.0032	0.3161	0.2988	-			
RGR_{GA}	21	**-0.4241***	**-0.8814*** **	**-0.4283***	**-0.6455*** **	0.0573	-		
RWR	22	0.1185	-0.5228**	-0.3283	0.2054	0.1855	0.3076	-	
Early SLA	23	0.2593	0.0967	-0.0118	0.2842	0.1716	-0.1077	0.1959	-
Time of maximum growth rate	24	-0.0041	0.2313	0.1719	0.1424	-0.2238	-0.2864	-0.1879	-0.0401
		17	18	19	20	21	22	23	24

Table App. 17a - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (high density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-							
50% emergence	2	0.111	-						
Time of spike emergence	3	**0.3993***	0.0452	-					
% stem loss	4	0.108	**0.4605***	0.2217	-				
ABGW	5	-0.3183	-0.0864	-0.2204	-0.2115	-			
Early green area	6	**-0.4829***	-0.1447	-0.2818	-0.2827	**0.7101*****	-		
Early height	7	**-0.4907****	-0.1191	**-0.5132****	**-0.4808***	0.3745	0.3184	-	
Early leaf angle	8	0.1555	0.0181	0.1998	0.2942	**-0.4314***	**-0.4031***	-0.2856	-
Early leaf counts	9	-0.1378	-0.0542	-0.2146	0.1238	**0.3917***	-0.0524	0.348	-0.2812
Early leaf length	10	**-0.4192***	-0.1795	-0.1062	-0.3618	0.2791	0.2311	**0.6057*****	0.1549
Early leaf width	11	-0.318	-0.0071	-0.2978	-0.2125	0.355	0.3728	**0.5384****	**-0.4169***
Final height	12	0.0166	-0.102	0.2389	-0.1043	0.2567	0.2565	0.0193	0.0648
Final stem counts	13	0.0644	**-0.5182****	-0.2737	**-0.833*****	-0.0666	-0.0102	0.3237	-0.0911
Flag leaf SLA	14	0.0035	-0.2908	0.2875	0.0285	-0.1781	-0.1665	-0.2244	0.3402
Flag leaf angle	15	-0.1493	0.2074	-0.0558	0.166	-0.093	0.0238	0.2316	-0.0203
Flag leaf area	16	**0.3849***	0.1712	**0.6759*****	0.25	-0.3072	-0.3208	**-0.4667***	0.1101
Flag leaf length	17	**0.4233***	0.0969	**0.5884****	0.2012	-0.2385	-0.2404	**-0.4745***	0.0719
Flag leaf width	18	0.3191	0.089	**0.5912****	0.223	-0.3292	-0.3023	**-0.4614***	-0.1013
Maximum stem count	19	**0.415***	0.1872	0.1766	0.6876	**-0.4367***	**-0.544****	**-0.496****	**0.4972****
LAR	20	**-0.451***	-0.0712	-0.2162	-0.1645	0.3092	**0.7195*****	0.3703	-0.341
LWR	21	**-0.3852***	0.0374	-0.0211	0.0033	0.3436	-0.1292	**0.4214***	-0.1124
Maximum growth rate	22	0.3737	-0.2222	**0.4228***	-0.0259	-0.0205	-0.2065	-0.2436	0.0639
NAR	23	0.166	-0.1611	0.1812	-0.193	0.3183	0.2629	-0.2349	0.221
RGR_{DWT}	24	**-0.4211***	-0.1926	-0.2395	-0.2575	**0.5406****	**0.713*****	0.1626	-0.1223
RGR_{GA}	25	-0.0706	-0.1651	-0.0843	-0.2171	-0.2196	0.3456	-0.1184	0.0934
RWR	26	0.0441	0.0053	0.1575	0.2313	-0.1332	0.136	**-0.4705***	**0.3953***
Early SLA	27	-0.0651	-0.0277	-0.116	-0.1353	-0.1836	**0.4688***	0.0458	-0.266
Rate of tillering	28	0.0587	0.0781	-0.192	0.2519	0.0664	-0.1377	0.1635	0.1551
Time of maximum growth rate	29	0.1927	-0.2068	**0.4261***	0.0923	0.0061	-0.3116	-0.3424	-0.0236
Time of maximum stem number	30	0.2968	0.1278	0.3258	**0.4148***	**-0.4666***	**-0.331***	**-0.6067*****	0.3244
Seed return per plant	31	**0.5706****	0.0545	**0.4419***	**0.4906****	-0.2269	-0.5024	-0.3793	**0.522****
Weed biomass per plant	32	0.3601	0.0163	**0.5019****	**0.531****	-0.1379	-0.3023	**-0.5215****	0.3252
		1	2	3	4	5	6	7	8

Table App. 17b - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (high density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Early leaf counts	9	-							
Early leaf length	10	0.1276	-						
Early leaf width	11	0.3268	**0.4763***	-					
Final height	12	-0.0824	**0.4341***	0.1251	-				
Final stem counts	13	-0.0501	0.1901	0.0132	-0.0252	-			
Flag leaf SLA	14	-0.0279	0.0287	-0.1363	0.2765	0.1426	-		
Flag leaf angle	15	-0.1934	-0.1449	-0.1436	0.03	-0.3211	-0.1583	-	
Flag leaf area	16	-0.237	-0.2256	-0.1272	0.192	-0.1748	**0.4027***	-0.0765	-
Flag leaf length	17	-0.2667	-0.2479	-0.175	0.169	-0.143	0.1882	-0.0321	**0.91*****
Flag leaf width	18	-0.1923	-0.2918	-0.1489	0.0553	-0.1411	0.1456	-0.1692	**0.8364*****
Maximum stem count	19	0.1452	-0.3685	-0.37	-0.2044	-0.2091	0.2712	-0.2144	0.2602
LAR	20	-0.0897	0.2328	**0.6113*****	-0.0224	-0.0598	-0.1685	-0.0188	-0.1667
LWR	21	**0.5179****	**0.3883***	0.3329	-0.1281	-0.0507	0.0892	-0.129	0.054
Maximum growth rate	22	0.0895	-0.0586	-0.1809	**0.6357*****	0.0358	0.2058	0.0265	0.3674
NAR	23	-0.2343	0.0217	**-0.4853***	**0.4481***	0.1228	0.1352	-0.0037	-0.057
RGR_{DWT}	24	-0.1229	0.1957	-0.0092	0.4145*	-0.0182	-0.104	0.2026	**-0.439****
RGR_{GA}	25	**-0.5677****	-0.0494	-0.176	0.2719	0.0834	-0.0297	0.2957	-0.1763
RWR	26	-0.3105	-0.2534	**-0.5319****	-0.0803	0.0521	0.2403	-0.2463	0.0912
Early SLA	27	**-0.4174***	-0.0835	0.3215	0.0014	0.0138	-0.2212	0.0966	-0.082
Rate of tillering	28	0.4748	-0.0193	0.3174	-0.3099	-0.1155	0.009	-0.0729	-0.2628
Time of maximum growth rate	29	0.0021	-0.1626	**-0.4275***	0.1408	-0.0931	0.3339	-0.0266	0.1955
Time of maximum stem number	30	-0.3433	-0.331	**-0.6012*****	0.0538	-0.125	0.2286	-0.0847	0.4527*
Seed return ($plant^{-1}$)	31	0.1905	-0.1894	**-0.4129***	0.0306	-0.3492	0.1683	0.0945	0.159
Weed biomass ($plant^{-1}$)	32	0.1353	-0.1522	-0.2686	0.2337	**-0.4377****	0.2741	-0.1001	0.3476
		9	10	11	12	13	14	15	16

Table App. 17c - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (high density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Flag leaf length	17	-							
Flag leaf width	18	**0.8309*** **	-						
Maximum stem count	19	0.191	0.1988	-					
LAR	20	-0.1988	-0.0831	**-0.4023***	-				
LWR	21	-0.0557	0.0647	-0.08	0.0674	-			
Maximum growth rate	22	0.4099*	0.2975	0.0322	-0.3374	-0.0866	-		
NAR	23	0.0628	-0.2204	-0.0939	**-0.394***	**-0.4222***	0.2957	-	
RGR_{DWT}	24	-0.3262	**-0.5035****	**-0.5039****	0.1389	-0.3661	0.0052	**0.6875*****	-
RGR_{GA}	25	-0.0776	-0.2108	-0.307	0.1109	**-0.8372*****	0.0385	**0.4431***	**0.6382*****
RWR	26	0.1131	0.0544	**0.514****	-0.0432	-0.3638	-0.1511	**0.4076***	0.1228
Early SLA	27	-0.0827	0.025	-0.2661	**0.7241*****	**-0.5556****	-0.2232	-0.2626	0.1432
Rate of tillering	28	**-0.4104***	**-0.3846***	0.3698	0.158	0.2774	-0.2444	**-0.4042***	-0.3202
Time of maximum growth rate	29	0.2213	0.1929	0.0475	**-0.4692***	0.1655	**0.3879***	0.2576	-0.0722
Time of maximum stem number	30	**0.5205****	**0.4877****	**0.5559****	**-0.4745***	-0.3758	0.1554	0.2845	-0.122
Seed return ($plant^{-1}$)	31	0.1278	-0.021	**0.5576****	**-0.5228****	-0.1129	0.3798	0.1919	-0.2383
Weed biomass ($plant^{-1}$)	32	0.2792	0.1862	**0.474***	-0.3625	-0.1287	0.4277	0.1902	-0.0831
		17	18	19	20	21	22	23	24

Table App. 17d - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (high density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

RGR_{GA}	25	-						
RWR	26	0.1901	-					
Early SLA	27	**0.581****	0.0459	-				
Rate of tillering	28	**-0.4526***	-0.0817	-0.0624	-			
Time of maximum growth rate	29	-0.1987	-0.024	**-0.4907****	-0.2526	-		
Time of maximum stem number	30	0.1958	**0.5513****	-0.1273	**-0.5523****	0.2089	-	
Seed return ($plant^{-1}$)	31	-0.1451	0.0615	-0.3693	0.2775	0.2892	0.2356	-
Weed biomass ($plant^{-1}$)	32	-0.0472	0.1002	-0.2278	0.0714	0.3167	0.3356	**0.7604*****
		25	26	27	28	29	30	31

Table App. 18a - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (low density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-							
Time of emergence	2	0.2656	-						
Time of spike emergence	3	0.2513	0.3604	-					
% Stem loss	4	0.3284	0.1004	**0.5155****	-				
ABGW	5	-0.231	-0.1247	-0.285	**-0.3833***	-			
Early green area	6	**-0.4032***	-0.1547	-0.3716	**-0.6157*****	**0.7478*****	-		
Early height	7	**-0.5028****	-0.3028	**-0.763*****	**-0.5688****	0.2933	**0.5198****	-	
Early leaf angle	8	0.2676	0.0257	-0.0137	0.2671	**-0.6469*****	**-0.4821****	-0.2138	-
Early leaf counts	9	-0.3714	-0.1296	-0.331	-0.2819	0.334	**0.4937****	**0.5732****	-0.1804
Early leaf length	10	-0.2612	0.0625	-0.2445	**-0.4764***	**0.4253***	**0.4339***	**0.3894***	**-0.5677****
Early leaf width	11	0.0494	-0.0008	**-0.4179***	**-0.5421****	**0.4089***	**0.5382****	**0.5532***	-0.2605
Final height	12	-0.1304	0.2851	0.3426	-0.2614	0.1331	0.0946	**-0.1643****	-0.0722
Final stem count	13	-0.1771	-0.2512	-0.3608	**-0.6497*****	0.0568	0.2697	0.3991	0.0062
Flag leaf SLA	14	0.1784	0.0404	**0.4177***	0.29	**-0.5946*****	**-0.4162***	**-0.3836***	0.1102
Flag leaf angle	15	0.3372	0.0703	-0.0208	0.0359	-0.1248	-0.0938	**-0.1335***	0.1213
Flag leaf area	16	0.0628	0.1709	**0.3986***	-0.078	0.1548	0.1003	-0.3066	-0.1411
Flag leaf length	17	0.1526	-0.0707	**0.459***	0.1283	0.0612	-0.0747	**-0.375***	0.0688
Flag leaf width	18	0.1017	0.0259	**0.5271****	0.1319	0.0655	-0.1244	**-0.38***	-0.1553
Maximum stem number	19	0.2626	-0.1865	0.2231	**0.6568*****	**-0.5622****	**-0.6179*****	-0.3529	**0.4785***
LAR	20	**-0.4359***	-0.2152	**-0.4464***	**-0.5087****	0.2654	**0.6756*****	**0.6159*****	-0.1981
LWR	21	**-0.3969***	-0.3149	-0.1034	0.0542	0.2401	-0.1704	0.0887	-0.2072
Maximum growth rate	22	0.4183*	0.2183	**0.4119***	**0.3816***	**-0.603*****	**-0.382***	-0.3541	0.3256
NAR	23	0.2097	0.137	0.2064	-0.0337	**0.4528***	**0.3744***	-0.254	**-0.0722**
RGR_{DWT}	24	-0.325	0.1404	-0.0842	-0.3791	**0.6378*****	**0.7565*****	0.2316	-0.3858*
RGR_{GA}	25	-0.0307	0.2728	0.0946	-0.2428	-0.1173	**0.3891***	0.0966	0.1089
RWR	26	0.0071	-0.2561	0.0335	0.1334	-0.1984	0.0696	-0.1687	**0.4093***
Early SLA	27	-0.0623	0.0818	-0.2622	**-0.4067***	-0.1853	**0.4288***	**0.4372***	0.0113
Rate of tillering	28	-0.0058	-0.1064	**-0.3983***	0.2212	-0.1595	-0.2046	0.1713	**0.4154***
Time of maximum growth rate	29	0.2714	0.0538	0.2053	0.3729	-0.3815	-0.3142	-0.2508	-0.0602
Time of maximum stem number	30	0.3144	-0.0729	**0.6616*****	**0.3975***	-0.2908	-0.294	**-0.5521****	-0.0237
Seed return per plant	31	0.3073	0.2554	0.2049	0.036	0.1363	0.0863	-0.1039	-0.0449
Weed biomass per plant	32	0.3037	**0.4448***	0.4759*	0.2986	-0.0583	-0.1504	-0.3609	-0.0089
		1	2	3	4	5	6	7	8

Table App. 18b - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (low density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Early leaf counts	9	-							
Early leaf length	10	0.3628	-						
Early leaf width	11	**0.5468****	**0.4635***	-					
Final height	12	0.156	0.2679	0.0828	-				
Final stem count	13	0.1381	-0.066	0.1777	0.1386	-			
Flag leaf SLA	14	-0.3736	-0.2366	**-0.3969***	-0.0147	-0.1401	-		
Flag leaf angle	15	-0.115	-0.2882	0.0681	-0.2526	0.1636	0.0491	-	
Flag leaf area	16	-0.1314	0.0419	-0.0617	0.3518	0.1627	0.037	-0.3447	-
Flag leaf length	17	-0.1331	-0.0083	-0.1499	0.268	-0.0373	0.0394	-0.3316	**0.7259*****
Flag leaf width	18	-0.0394	0.1395	-0.0782	0.3118	-0.1408	0.0311	**-0.4135***	**0.5715****
Maximum stem number	19	-0.2449	**-0.6481*****	**-0.5265****	-0.232	0.0584	0.2846	0.1495	0.0053
LAR	20	**0.5872****	**0.5919*****	**0.5773****	-0.0145	0.0737	-0.2474	-0.3075	-0.0966
LWR	21	0.1455	0.2815	-0.0761	0.0919	-0.1894	-0.2496	**-0.4797****	0.0527
Maximum growth rate	22	-0.3204	-0.2009	-0.2421	-0.0403	-0.1649	**0.5426****	0.1541	-0.0612
NAR	23	-0.183	-0.3081	-0.1106	0.1756	0.146	-0.1391	0.2183	0.2472
RGR_{DWT}	24	0.1792	0.1005	0.1539	0.1936	0.2	-0.2964	0.1301	0.0641
RGR_{GA}	25	-0.008	-0.125	0.0764	0.0686	0.2127	0.1869	0.3147	-0.086
RWR	26	-0.0839	**-0.5616****	-0.3405	-0.101	0.3333	0.1438	0.0499	0.2505
Early SLA	27	0.3199	0.3074	0.4874**	-0.0944	0.1579	0.112	0.0272	-0.173
Rate of tillering	28	0.0188	-0.3814*	**-0.0927**	-0.3247	0.1356	**-0.2637****	0.0136	-0.0922
Time of maximum growth rate	29	-0.2497	-0.2137	-0.2075	**-0.4327***	-0.1837	**0.4974****	0.2537	-0.1125
Time of maximum stem number	30	-0.3418	-0.229	**-0.4221***	0.1151	-0.0952	0.5605	0.1619	0.1127
Seed return ($plant^{-1}$)	31	-0.1634	0.1087	0.0261	0.2035	-0.0999	-0.164	0.0679	0.2577
Weed biomass ($plant^{-1}$)	32	-0.1372	0.0062	-0.1159	0.4586	-0.1611	0.113	-0.052	**0.5062****
		9	10	11	12	13	14	15	16

Table App. 18c - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (low density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Flag leaf length	17	-							
Flag leaf width	18	**0.8013*** **	-						
Maximum stem number	19	0.1817	0.0931	-					
LAR	20	-0.1094	-0.0206	**-0.4807** **	-				
LWR	21	0.2753	**0.4504***	-0.0278	0.0612	-			
Maximum growth rate	22	0.1976	0.1726	**0.3821***	-0.0924	-0.3617	-		
NAR	23	0.1648	-0.0707	-0.0932	-0.3405	**-0.4424***	-0.1277	-	
RGR_{DWT}	24	-0.1854	-0.3353	**-0.4978** **	0.131	**-0.3902***	-0.3605	**0.7379*** **	-
RGR_{GA}	25	-0.2683	**-0.4682***	-0.2297	0.1442	**-0.8549*** **	0.2386	**0.457***	**0.6253*** **
RWR	26	0.189	0.037	**0.55** **	-0.0746	-0.3418	0.1164	0.3391	0.0803
Early SLA	27	-0.3433	-0.3023	-0.3087	**0.7279*** **	**-0.5441** **	0.265	-0.2442	0.1153
Rate of tillering	28	-0.0937	-0.1237	**0.5408** **	-0.049	0.1043	-0.0446	-0.1931	-0.2816
Time of maximum growth rate	29	-0.013	0.1549	0.2894	-0.1297	-0.0949	**0.5774** **	-0.2291	**-0.3846***
Time of maximum stem number	30	0.2838	0.2539	0.3727	**-0.4039***	-0.2261	0.4738*	0.2427	-0.0831
Seed return ($plant^{-1}$)	31	0.2463	-0.0506	-0.1015	-0.1517	-0.3379	0.1625	**0.395***	0.2913
Weed biomass ($plant^{-1}$)	32	**0.3772***	0.2354	0.2423	-0.3062	-0.2399	0.176	0.2649	0.0678
		17	18	19	20	21	22	23	24

Table App. 18d - Pearson's correlations coefficients of traits in the 2013-14 sand-beds experiment (low density treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

RGR_{GA}	25	-						
RWR	26	0.2108	-					
Early SLA	27	**0.5927*** **	0.033	-				
Rate of tillering	28	-0.3229	**0.4636***	-0.1213	-			
Time of maximum growth rate	29	-0.0523	0.0204	0.0991	-0.0415	-		
Time of maximum stem number	30	0.1816	0.1118	-0.1517	**-0.536****	0.3232	-	
Seed return per plant	31	0.2797	-0.0484	-0.007	-0.1805	-0.2893	0.1588	-
Weed biomass per plant	32	0.0821	0.1688	-0.1378	0.0541	-0.1827	0.2062	**0.642*****
		25	26	27	28	29	30	31

Table App. 19a - Pearson's correlations coefficients of traits in the 2011-12 field experiment. * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-							
ABGW	2	**0.6669****	-						
A. myo biomass (m^2)	3	-0.0803	-0.2018	-					
A. myo biomass ($plants^{-1}$)	4	-0.216	-0.0232	-0.2553	-				
Early height	5	-0.2292	-0.1161	0.1877	-0.053	-			
Final stem number	6	-0.2952	-0.3939	-0.338	0.0895	0.0263	-		
Flag leaf SLA	7	-0.1126	0.276	-0.162	0.3504	0.1839	-0.1022	-	
Flag leaf angle	8	**-0.4446***	-0.4174	-0.0523	0.045	-0.2068	-0.291	0.0192	-
Flag leaf length	9	-0.019	-0.2052	0.0846	-0.0519	**0.5467***	0.3535	0.1721	-0.2202
Flag leaf width	10	**-0.51***	**-0.5292***	0.0456	0.3655	0.3452	**0.5586***	0.3487	-0.1392
Harvest index	11	0.3341	0.2944	-0.2941	0.0417	-0.2271	-0.1162	-0.1561	-0.1353
Final height	12	-0.0969	-0.1774	-0.1057	0.4365	0.1586	0.3995	0.3215	-0.1824
Maximum stem count	13	-0.0554	-0.057	-0.3902	**0.4541***	0.0854	**0.6105****	0.1593	-0.2906
Early leaf area	14	**0.7468*****	**0.9274*****	-0.2719	0.0572	-0.1291	-0.3538	0.3171	-0.3902
Early leaf number	15	-0.3631	-0.2385	-0.2994	0.0711	-0.4106	0.0438	-0.057	**0.6152****
Time of max. stem number	16	0.2723	0.095	0.0417	0.1272	0.3528	0.0493	0.2408	-0.3841
Rate of tillering	17	-0.2906	-0.1052	-0.1123	0.0247	-0.2966	0.0236	-0.1991	0.3789
Early SLA	18	0.4428	0.2867	-0.3673	0.3748	-0.068	0.0256	0.3943	-0.1573
Seed return (m^2)	19	0.1061	-0.2216	**0.7503*****	-0.2183	-0.1627	-0.346	-0.3213	0.0237
Tolerance residual	20	0.0088	**-0.459***	-0.0102	**-0.4711***	0.0377	**0.5142***	-0.3477	0.0288
Early green area	21	**0.7253*****	**0.9308*****	-0.2622	0.0819	-0.1355	-0.3487	0.3262	-0.3989
Stem loss	22	0.2927	0.3717	-0.0489	0.3404	0.0978	**-0.5418***	0.2533	0.0236
Wheat biomass	23	0.0209	-0.0612	**-0.7623*****	**0.4568***	-0.3125	**0.6151****	-0.0338	-0.0852
Flag leaf area	24	-0.2417	-0.2221	-0.0334	**0.6638****	0.2562	0.1541	**0.5237***	0.0196
Time of max. growth rate	25	**-0.4893***	**-0.6826*****	0.2277	-0.0658	0.4181	0.1646	-0.1245	0.1955
Seed return ($plant^{-1}$)	26	-0.0781	-0.1957	0.054	**0.7036*****	-0.2876	-0.1037	0.0162	0.1492
		1	2	3	4	5	6	7	8

Table App. 19b - Pearson's correlations coefficients of traits in the 2011-12 field experiment. * = P<0.05; **=P<0.01; ***=P<0.001.

Flag leaf length	9	-							
Flag leaf width	10	**0.4818***	-						
Harvest index	11	**-0.5055***	-0.2317	-					
Final height	12	**0.4899***	0.4365	-0.3909	-				
Maximum stem count	13	0.3103	**0.5081***	-0.1411	**0.4635***	-			
Early leaf area	14	-0.172	**-0.4618***	0.2598	-0.0538	-0.0014	-		
Early leaf number	15	**-0.4823***	-0.1268	0.222	-0.1927	-0.2096	-0.2472	-	
Time of max. stem number	16	**0.4893***	0.357	-0.158	0.1819	**0.5927****	0.0946	**-0.536***	-
Rate of tillering	17	**-0.5419***	-0.2033	0.1727	-0.093	-0.3563	-0.0649	**0.755*****	**-0.8207*****
Early SLA	18	0.0912	0.0655	0.0891	0.2717	0.2615	**0.5792****	0.0104	0.2145
Seed return (m^2)	19	-0.1431	-0.1328	-0.0072	-0.0901	-0.4151	-0.2888	-0.0419	-0.0236
Tolerance residual	20	0.4396	0.2305	-0.1779	0.0734	0.1403	-0.348	0.1548	0.0648
Early green area	21	-0.1967	-0.4333	0.274	-0.0547	0.0269	**0.9971*****	-0.2453	0.1
Stem loss	22	-0.0722	-0.1366	-0.0455	0.0409	0.3202	0.3959	-0.2926	**0.5774****
Wheat biomass	23	0.1165	0.1644	0.1354	0.4341	**0.5427***	**0.0459***	0.1652	-0.0672
Flag leaf area	24	**0.4823***	**0.6425****	-0.1183	**0.6352****	0.3275	-0.1623	-0.1434	0.2836
Time of max. growth rate	25	0.1365	0.2578	-0.0821	0.0748	-0.179	**-0.7082*****	0.1572	0.0041
Seed return ($plant^{-1}$)	26	-0.2369	0.1408	0.1689	0.3083	0.1359	-0.1645	0.2197	0.0289
		9	10	11	12	13	14	15	16

Table App. 19c - Pearson's correlations coefficients of traits in the 2011-12 field experiment. * = P<0.05; **=P<0.01; ***=P<0.001.

Rate of tillering	17	-								
Early SLA	18	-0.0147	-							
Seed return (m^2)	19	-0.0001	-0.344	-						
Tolerance residual	20	0.027	0.0945	-0.0494	-					
Early green area	21	-0.0527	**0.5656****	-0.2896	-0.3684	-				
Stem loss	22	-0.4243	0.2386	-0.0457	**-0.4483***	0.4139	-			
Wheat biomass	23	0.0762	0.3626	**-0.5643****	0.1963	0.0415	-0.1475	-		
Flag leaf area	24	-0.2681	0.232	-0.1564	-0.0939	-0.1515	0.1405	0.3129	-	
Time of max. growth rate	25	-0.0336	-0.2997	0.2072	0.1964	**-0.7316*****	-0.3267	-0.162	0.1909	-
Seed return ($plant^{-1}$)	26	0.1172	0.1131	**0.4569***	-0.3889	-0.1496	0.2414	0.1781	0.396	0.0851
		17	18	19	20	21	22	23	24	25

Table App. 20a - Pearson's correlations coefficients of traits in the 2011-12 field experiment (early drill treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-							
% Yield loss	2	-0.0585	-						
ABGW	3	-0.0394	0.2045	-					
A. myosuroides dry weight (g m^2)	4	0.0062	0.0977	0.2471	-				
A. myosuroides dry weight (g $plant^{-1}$)	5	-0.0755	**0.6943*** **	0.2327	**0.6605*** **	-			
Early height	6	**-0.5646** **	0.345	0.2344	0.0296	0.2795	-		
Final stem count	7	**-0.567** **	**0.3995***	0.3446	0.3609	**0.454***	**0.5263** **	-	
Flag leaf SLA	8	-0.0027	-0.1886	-0.0541	-0.1681	-0.3047	-0.0695	-0.1846	-
Flag leaf angle	9	-0.1632	-0.2163	0.1908	0.1113	-0.1399	-0.1029	0.102	0.0951
Flag leaf length	10	0.0708	0.1538	0.281	-0.0452	0.1273	0.2744	0.1796	-0.1647
Flag leaf width	11	-0.0866	0.1084	0.3111	-0.0325	0.2639	0.2812	**0.4252***	-0.2142
Harvest index	12	-0.1258	-0.014	-0.1195	0.1207	-0.0406	0.0164	0.2537	0.3097
Final height	13	-0.0622	-0.1305	0.3613	0.1776	0.2026	0.2779	0.1153	-0.2032
Maximum stem number	14	**0.3842***	0.0223	**0.4226***	-0.0196	-0.1244	-0.3105	0.1496	-0.0999
Early leaf area	15	-0.3143	0.1216	**0.9088*** **	0.1221	0.1064	0.3667	**0.4354***	-0.0751
Early leaf number	16	0.2242	0.1851	**0.6856*** **	0.2793	0.2468	-0.1415	0.1176	0.2263
Time of maximum stem number	17	0.1038	-0.2157	-0.1296	-0.1906	-0.3051	0.0135	-0.1762	-0.1059
Rate of tillering	18	0.0997	0.2565	0.3637	0.1577	0.2388	-0.1787	0.2357	0.0376
Early SLA	19	**-0.5056** **	-0.122	0.0876	-0.1824	-0.2146	**0.4112***	0.1362	0.0042
Seed return (m^2)	20	0.0281	-0.0846	**0.4877** **	**0.4103***	0.066	-0.0362	0.1325	0.2263
Early green area	21	-0.3193	0.1482	**0.9111*** **	0.1292	0.1263	**0.3682***	**0.4404***	-0.1036
% Stem loss	22	**0.7138*** **	-0.2851	0.054	-0.2949	**-0.4425***	**-0.6307*** **	**-0.609*** **	0.0634
Weed-free yield	23	-0.0968	-0.1694	0.0737	0.1779	0.0364	-0.085	0.0425	**-0.3702***
Final wheat biomass (m^2)	24	-0.0598	0.1965	-0.1454	-0.0899	0.2731	0.23	0.2854	-0.2467
Flag leaf area	25	0.0089	0.2577	0.2688	-0.0329	0.2011	0.2666	0.3182	-0.1989
Time of maximum growth rate	26	0.0177	0.1258	**0.5936*** **	0.2589	0.1595	0.0458	0.2762	-0.0816
Seed return ($plant^{-1}$)	27	-0.0949	**0.5246** **	**0.5466** **	0.3356	**0.5548** **	0.2143	0.2959	0.027
		1	2	3	4	5	6	7	8

Table App. 20b - Pearson's correlations coefficients of traits in the 2011-12 field experiment (early drill treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Flag leaf angle	9	-							
Flag leaf length	10	-0.3353	-						
Flag leaf width	11	-0.2908	**0.5986*** **	-					
Harvest index	12	0.2032	**-0.513** **	-0.2031	-				
Final height	13	-0.1978	**0.5465** **	0.213	**-0.4404***	-			
Maximum stem number	14	-0.036	0.239	0.2796	-0.0989	0.0811	-		
Early leaf area	15	0.3193	0.1917	0.2306	-0.0994	0.2874	0.3066	-	
Early leaf number	16	0.0323	0.1423	0.1049	0.0058	0.1281	**0.419***	**0.4569***	-
Time of maximum stem number	17	-0.272	0.1727	-0.1254	0.0454	0.0604	0.03	-0.1703	-0.2184
Rate of tillering	18	0.3159	-0.0517	0.2215	-0.1117	-0.0765	**0.4864** **	0.3473	**0.4496***
Early SLA	19	0.1522	0.0947	-0.2934	0.0253	0.0041	-0.2023	**0.3786***	-0.1687
Seed return (m^2)	20	0.1762	-0.1037	-0.2118	0.22	0.085	0.3474	**0.3767***	**0.4733** **
Early green area	21	0.3072	0.2188	0.2402	-0.1082	0.2893	0.3053	**0.9956*** **	0.4599*
% Stem loss	22	-0.0982	0.0852	-0.0693	-0.2825	-0.0262	**0.6832*** **	-0.0923	0.2257
Weed-free yield (kg m^2)	23	0.1303	0.0549	-0.3482	-0.291	0.2549	0.1942	0.1452	0.1263
Final wheat biomass (m^2)	24	-0.1244	0.08	0.3237	0.325	0.0561	-0.2226	-0.1607	-0.0728
Flag leaf area	25	-0.3087	**0.902*** **	**0.8481*** **	**-0.4344***	**0.4494***	0.2544	0.1731	0.0683
Time of maximum slope	26	0.3049	0.2262	**0.4933** **	-0.2445	0.0619	**0.4205***	**0.6027*** **	0.2457
Seed return ($plant^{-1}$)	27	-0.0399	0.063	0.0543	0.0612	0.1559	0.2181	**0.4164***	**0.4968** **
		9	10	11	12	13	14	15	16

Table App. 20c - Pearson's correlations coefficients of traits in the 2011-12 field experiment (early drill treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Time of maximum stem number	17	-									
Rate of tillering	18	**-0.8246*** **	-								
Early SLA	19	0.1318	-0.1992	-							
Seed return (m^2)	20	-0.0528	0.2302	-0.0066	-						
Early green area	21	-0.148	0.3287	**0.3745***	**0.3794***	-					
% Stem loss	22	0.1546	0.2236	-0.2452	0.1613	-0.0978	-				
Weed-free yield (kg m^2)	23	-0.0919	0.2106	0.261	0.2936	0.1693	0.1299	-			
Final wheat biomass (m^2)	24	-0.0148	-0.125	-0.1308	**-0.4361***	-0.1574	**-0.3875***	-0.1917	-		
Flag leaf area	25	0.058	0.0552	-0.1608	-0.1683	0.1951	-0.0061	-0.156	0.1938	-	
Time of maximum slope	26	-0.3275	**0.5211** **	-0.0786	0.1892	**0.5928*** **	0.1211	-0.1006	-0.2404	**0.39***	-
Seed return ($plant^{-1}$)	27	-0.1859	0.321	-0.0338	**0.7212*** **	**0.4393***	-0.0635	0.2328	-0.1512	0.0426	0.1426
		17	18	19	20	21	22	23	24	25	26

Table App. 21a - Pearson's correlations coefficients of traits in the 2011-12 field experiment (late drill treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

TGW	1	-							
% Yield loss	2	-0.2413	-						
ABGW	3	-0.0577	-0.4327	-					
A. myosuroides biomass (m^2)	4	0.0218	0.344	0.2387	-				
A. myosuroides biomass ($plant^{-1}$)	5	-0.0771	**0.7678*** **	-0.1874	**0.7582*** **	-			
Early height	6	-0.0696	-0.2859	**0.5727***	0.079	-0.1511	-		
Final stem count	7	0.3981	**-0.5287***	-0.1416	-0.2754	-0.3767	-0.1721	-	
Flag leaf SLA	8	**0.5391***	0.037	-0.3434	0.3628	0.2516	-0.2411	**0.4697***	-
Flag leaf angle	9	-0.2789	0.2071	-0.1737	-0.2605	-0.1282	-0.0864	-0.1208	-0.1209
Flag leaf length	10	**0.4996***	-0.2945	-0.0981	-0.2387	-0.3014	-0.0665	0.4428	0.2506
Flag leaf width	11	0.2795	-0.1619	-0.1429	-0.235	-0.1342	-0.3787	0.4141	0.0928
Harvest Index	12	0.0077	**-0.5739***	0.4663	-0.0673	**-0.4811***	-0.1282	0.1172	-0.108
Fiinal height	13	0.1663	-0.0106	-0.0963	-0.4069	-0.2037	0.3017	-0.0029	-0.221
Maximum stem number	14	-0.1452	0.1103	0.3335	0.3559	0.1272	0.4835*	-0.4072	-0.0859
Early leaf area	15	-0.2947	-0.0841	**0.8153*** **	0.1331	-0.0258	0.3649	-0.3174	**-0.6159** **
Early leaf number	16	0.0179	-0.2917	**0.7442*** **	0.1642	-0.2105	0.419	-0.0849	-0.3198
Time of maximum stem number	17	-0.3907	0.2632	0.2206	0.4408	0.2849	0.4065	-0.3567	0.0621
Rate of tillering	18	0.3652	-0.2258	-0.1294	-0.3268	-0.2232	-0.2597	0.1513	-0.1712
Early SLA	19	-0.1771	0.1277	0.0373	-0.2584	-0.0276	-0.0184	-0.2367	**-0.636** **
A. myosuroides seed return (m^2)	20	-0.0247	**0.4848***	0.1831	**0.8097*** **	**0.7006** **	-0.0667	**-0.5769***	0.0569
Early green area	21	-0.2853	-0.0871	**0.853*** **	0.1577	-0.0374	0.3983	-0.3445	**-0.5843***
% stem loss	22	-0.2787	0.3644	0.2739	0.3288	0.2807	0.417	**-0.85*** **	-0.3554
Wheat-free yield (kg m^2)	23	-0.3574	-0.0278	0.442	-0.0957	-0.1468	0.2393	-0.3969	**-0.6002** **
Wheat biomass (m^2)	24	0.4181	-0.3848	0.1558	-0.227	-0.3619	0.3307	0.3737	0.1254
Flag leaf area	25	0.3717	0.0268	-0.3572	-0.129	0.0346	-0.2644	0.3245	0.3132
Time of maximum growth rate	26	**0.4971***	-0.3556	0.2954	-0.1655	-0.3039	0.0685	-0.063	0.0403
A. myosuroides seed return ($plant^{-1}$)	27	-0.1459	**0.7709*** **	-0.1155	**0.6302** **	**0.8567*** **	-0.2009	**-0.6165** **	-0.0061
		1	2	3	4	5	6	7	8

Table App. 21b - Pearson's correlations coefficients of traits in the 2011-12 field experiment (late drill treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Flag leaf angle	9	-							
Flag leaf length	10	-0.4093	-						
Flag leaf width	11	-0.3561	**0.7546*** **	-					
Harvest Index	12	-0.0727	-0.0933	-0.0743	-				
Fiinal height	13	-0.2951	0.3561	0.041	-0.1723	-			
Maximum stem number	14	-0.4466	0.0341	-0.2683	-0.0317	0.3107	-		
Early leaf area	15	-0.0204	-0.3698	-0.1666	0.2286	-0.1328	0.211	-	
Early leaf number	16	-0.2114	0.1098	-0.0997	0.2767	0.0028	0.4348	**0.6397****	-
Time of maximum stem number	17	-0.0736	-0.0399	-0.2366	-0.1466	0.0676	**0.7307*** **	0.0475	0.1137
Rate of tillering	18	-0.2514	0.0198	0.0649	0.1449	0.1328	-0.2418	0.0416	0.1799
Early SLA	19	0.1734	-0.2956	-0.0893	-0.1728	-0.0329	-0.31	**0.4641***	0.1312
A. myosuroides seed return (m^2)	20	-0.0184	-0.2731	-0.2456	-0.0703	-0.4099	0.2136	0.2004	0.0876
Early green area	21	-0.0054	-0.3575	-0.1936	0.265	-0.1307	0.253	**0.9916*** **	**0.6791****
% stem loss	22	-0.2093	-0.2439	-0.3723	-0.1256	0.2094	**0.8082*** **	0.3301	0.29
Wheat-free yield (kg m^2)	23	0.1255	**-0.4924***	**-0.5716***	0.2463	0.1487	0.3449	**0.6236****	0.4115
Wheat biomass (m^2)	24	-0.0678	**0.5373***	0.1636	0.1324	**0.6152****	0.1143	-0.1869	0.0337
Flag leaf area	25	-0.4195	**0.803*** **	**0.8449*** **	-0.2765	0.2912	-0.1304	**-0.4724***	-0.3296
Time of maximum growth rate	26	-0.3235	0.3046	0.158	0.2443	0.1846	0.1009	0.1373	0.3568
A. myosuroides seed return ($plant^{-1}$)	27	0.0932	-0.3319	-0.2025	-0.3614	-0.2611	0.0803	0.0794	-0.1865
		9	10	11	12	13	14	15	16

Table App. 21c - Pearson's correlations coefficients of traits in the 2011-12 field experiment (late drill treatment). * = P<0.05; **=P<0.01; ***=P<0.001.

Time of maximum stem number	17	-									
Rate of tillering	18	**-0.8105*** **	-								
Early SLA	19	**-0.5756***	**0.5449***	-							
A. myosuroides seed return (m^2)	20	0.294	-0.249	0.0509	-						
Early green area	21	0.1094	-0.0144	0.3818	0.215	-					
% stem loss	22	0.5726	-0.1649	0.0142	0.4284	0.3662	-				
Wheat-free yield (kg m^2)	23	**0.0595***	0.2056	0.4035	0.1231	**0.6116****	0.42	-			
Wheat biomass (m^2)	24	0.1077	-0.1814	-0.3485	-0.2763	-0.1635	-0.169	-0.0571	-		
Flag leaf area	25	-0.0579	-0.0967	-0.2873	-0.156	**-0.4776***	-0.2425	**-0.6798****	0.3284	-	
Time of maximum growth rate	26	-0.2406	0.4187	-0.0315	-0.1771	0.1645	0.1507	0.0109	0.0744	0.0401	-
A. myosuroides seed return ($plant^{-1}$)	27	0.2442	-0.2321	0.1721	**0.8755*****	0.0682	0.3838	0.0896	-0.3503	-0.0735	-0.2986
		17	18	19	20	21	22	23	24	25	26