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Identifying and evaluating competitive traits in wheat for sustainable weed management

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CONTENTS

1.	ABSTRACT	1
2.	INTRODUCTION	2
3.	MATERIALS AND METHODS	7
3.1.	Heading 2 style (please use the 'Styles' in the panel above so that the automatic table of contents updates correctly)	Error! Bookmark not defined.
3.1.1.	Heading 3 style	Error! Bookmark not defined.
4.	RESULTS	21
5.	DISCUSSION	38
6.	REFERENCES	41

1. 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.

2. Introduction

2.1. Weed 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. Weeds have been reported as the most importance pest problem in wheat (*Triticum aestivum* L.) production and are able to inflict a 34% potential yield loss on the crop globally (Oerke, 2006).

2.1.1. Weed management in the UK

The introduction of herbicides allowed very effective and relatively cheap control of weed species. Unfortunately, herbicide resistance is now widespread amongst many problematic weed species (Heap, 1997; 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).

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). Farmers have the option of using more competitive crop cultivars to suppress weed populations. The use of competitive cultivars and the interactions with other cultural control options will be addressed in this report.

2.1.2. 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.

Studies comparing the competitive ability of different cultivars are common (Andrew *et al.*, 2015) but are 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, we must identify the traits that determine the competitive ability of cultivars.

2.1.3. 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 with a seed decline rate of 80% per year. It is a well-studied species that causes significant yield losses in winter-sown cereal crops (Moss, 1987) with widespread resistance to many herbicides in many North-Western European countries (Lutman *et al.*, 2013; Moss *et al.*, 2011).

2.2. The role of traits in competitive ability

2.2.1. Defining a trait

In ecology, the term 'trait' indicates a 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 study will adhere to this definition where feasible.

2.2.2. 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).

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). Additionally, the taller cultivars are lower yielding in weed-free scenarios, making height an unpopular trait.

2.2.3. Early vigour

Early vigour of a cultivar is related to crop establishment and the rate at which aboveground material is produced, and has 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). In essence, high early vigour allows a crop to smother a weed.

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).

2.2.4. 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, and can vary between cultivars (Huel & Hucl, 1996; Seavers & Wright, 1997; Champion *et al.*, 1998). If stem 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). 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.

2.2.5. 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 measures of canopy architecture, concluding 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. rigidum* with growth habit or associated traits such as plant height and tiller number.

In some cases, a PAR (Photosynthetically Active Radiation) 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).

2.3. 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.

2.3.1. 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). The primary germination window for *A. myosuroides* is September and early October, with a small flush common in the spring. Delaying drilling until as late as November can substantially reduce *A. myosuroides* emergence.

Farmers are often unwilling to delay autumn sowing, as it 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 (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). 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.

2.3.2. Sowing rate

Increased sowing rate works on the principle that a greater mass of crop is present to compete against weeds. 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). Many studies have found that sowing rate did not change the competitive rankings of cultivars in wheat (Cousens & Fletcher, 1990; Kirkland & Hunter, 1991), 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. 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).

2.4. Project aims

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.

3. Materials and methods

3.1. Cultivar choice and seed sourcing

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 Epton, 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. 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.

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.

3.2. The sand-beds experiment

3.2.1. Experimental set-up

Container-based experiment

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 supplementary watering. There were three replicates of each cultivar, and these were arranged in fully randomised blocks. The experiment included containers that were sown with seeds that may be transplanted into experimental containers should individuals fail to establish. In 2013-14, 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. Table 3.1 provides a synopsis of the changes between experiments.

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. 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 20 mm depth in a pattern to replicate the standard drill pattern in the field (Figure 3.1). Pre-germinated *A. myosuroides* seedlings with no more than ~5 mm radicle growth were selected and were planted systematically in each container. Following 2011-12, *A. myosuroides* ten was removed from the experiment as it benefitted from an edge effect.

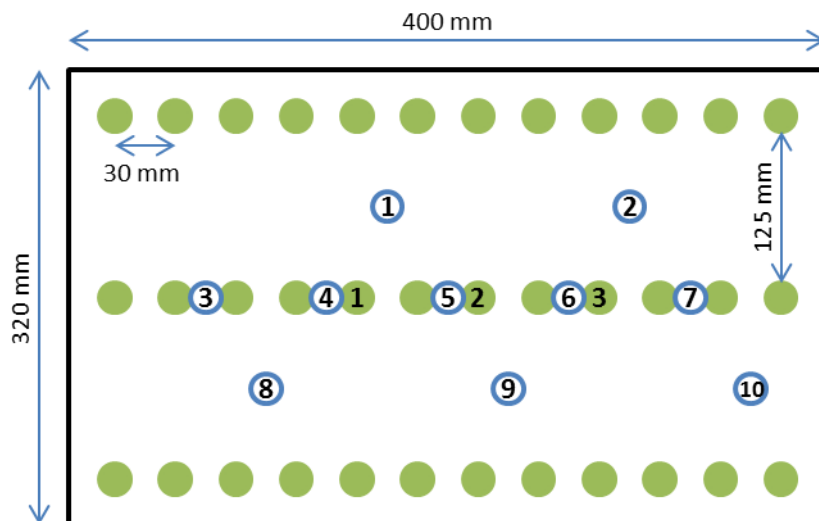


Figure 3.1 - Arrangement of species within containers in the 2011-12 experiment, with sampled individuals numbered. ● are cultivars, ○ are *A. myosuroides*.

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 date
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
Low density	257 x 356 x 162	117.86	196.74	98.4	14-15 Oct 2013

3.2.2. Data collection

Stem counts and height measurements

Cultivar height was measured weekly every one or two weeks from the soil to the highest point (without artificial interference) using a ruler. 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.

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.

Spike emergence

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. From this, time of 75% spike emergence was quantified.

Weed fitness

Seed heads were collected 7 - 14 June 2012, 17 - 21 June 2013, and 28 May - 4 June 2014 and stored in a drying room. Once dry, three seed heads were selected from each replicate, their length was measured and seeds counted. The total length of seed heads was measured and multiplied by seed per mm to obtain an approximate total seed return for 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 was dried at 80°C for at least an 18 hr period before weighing.

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. 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 using the WinDIAS programme and weighing the leaves after drying at 80°C overnight. Flag leaf angle was measured on 12 July 2013 and 5 June 2014.

Thousand grain weight (TGW)

One thousand grains of the planted seed were counted using an electronic grain counter, dried at 105°C for 18 hr and weighed. Three replicates for all cultivars were carried out, except Maris Widgeon, with only two replicates of dry weight due to limited seed being available.

3.2.3. Statistical analysis

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 1.

$$ptt = \Sigma \left((T_i - T_b) \times ((P_i - P_b)/24) \right) \quad (1)$$

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

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.

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. As each container represents a replicate, the individual plants must be treated as pseudo-replicates. Additionally, the data represent repeated measures. 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. 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:

$$y = a + \frac{c}{(1 + t \exp(-b(x - m)))^{\left(\frac{1}{t}\right)}} \quad (2)$$

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:
$$\frac{dy}{dx} = \frac{bc \exp(-b(x - m))}{(1 + t \exp(-b(x - m)))^{\left(\frac{1+t}{t}\right)}} \quad (3)$$

Maximised when $x = m$:
$$\max\left(\frac{dy}{dx}\right) = \frac{bc}{(1 + t)^{\left(\frac{1+t}{t}\right)}} \quad (4)$$

Heights from an approximate 120 ppt point were selected for use as a measure of early cultivar height across all years (approximately GS 13 – the stage at which three leaves have unfolded).

Modelling tiller production and loss

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. 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.

Partial redundancy analysis

Partial redundancy analysis (RDA), with year as a covariate, was employed to identify groups of traits that are primary drivers of differences between cultivars combining data from all years and for comparing treatments. 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. Only data from wheat cultivars were included in final analyses as differences between species of crop tended to dominate axes one and two. 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.

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. Seed return was normalised via logarithm to base ten to improve residuals.

The traits LAR and RGR_w were 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.

3.3. The field experiment

Only wheat cultivars were included in the field experiment due to complications in managing an experiment with multiple crop species.

3.3.1. 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 in both years, but was only achieved in 2013-14. 'Weed-free' plots were maintained to enable a comparison of final yield between cultivars when growing under *A. myosuroides* infestation. Sub-plot sizes were 9 x 3m (27 m²). Each plot was separated by a 1.5 m buffer and a 15 m discard between replicates.

Cultivars were drilled at a density of 350 seeds m⁻². *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. The seed had a 45% germination rate. The average weight of 100 seed 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/m². 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.

3.3.2. Data collection

Many traits were collected in the same manner as described in 3.2.2. Dates of data collection are presented in table 3.2.

Density counts

Density counts for the cultivars and *A. myosuroides* were conducted on all 'weedy' subplots. *Alopecurus myosuroides* were counted in six quadrats (0.25 m² in 2012-13, 0.5 m² 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 and *A. myosuroides* were counted following the spring flush. In the 2012-13 experiment, the background level of *A. myosuroides* was higher than anticipated, resulting in infestation in all plots and at inconsistent densities. Density counts were conducted in 'weed-free' subplots on 10 June 2013.

Table 3.2 - 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.

Data collection	2013	2014	
	Early drill treatment	Early drill treatment	Late drill treatment
Sowing date	02-Oct	04-Oct-13	24-Oct-13
Wheat density counts	29-Nov	26-Oct-13	06-Dec-13
<i>A. myo</i> density counts	21 Feb*	05-Mar-14	
Sampling for early vigour	05-Feb	21-Jan-14	19-Feb-14
Stem counts/crop height	Began 14 Nov 2012	Began 29-Oct-13	Began 25-Nov-13
Early height	08-Jan	25-Nov-13	08-Jan-14
Leaf counts	09-Jan	21-Jan-14	19-Feb-14
Biomass harvest	9-10 July	25 June - 10 July 2014	
Grain harvest	20-Aug	19-20 Aug 2014	

Early vigour traits

At approximately growth stage 21-23, 10 wheat individuals were removed from each plot at ground level. The material was stored in a 4°C room prior to assessment. The area of leaves and green stems was measured with WinDIAS software. Leaves and stem material were dried at 80°C overnight before being weighed.

Ecophysiological traits relevant to resource allocation and life history strategy were calculated (see section 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.

Height measurements and stem counts

Stem counts and crop height measurements were taken monthly. Ten individuals were selected at least one metre from the edge of each split-plot and measured as described in 3.2.2. Early cultivar height were measured at a similar photothermal time for each year (185.5 ptt on 8 January 2013, 185.5 ptt (25 November 2013) in the early drilled plots and 172.5 ptt (8 January 2014) in the late drilled plots). Final stem counts were taken from 18 July 2012 in 2012-13, and on 30 May 2014 in 2013-2014.

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. All plant material above ground level from three 0.25m² 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, 0.5m² quadrats were used. The plant material was separated into wheat and *A. myosuroides*. Wheat grain heads were collected and ear index was calculated. All seed heads were removed from *A. myosuroides* and placed in a drying room, and seed numbers were estimated as described in section 3.3.2. 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. Due to the

high background levels of *A. myosuroides*, it was not possible to acquire a ‘weed-free’ yield measure for 2012-13. Flag leaf angle, length, width and SLA were measured as described in section 3.2.2.

3.3.3. 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 m² 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). Seed return per plant was square root transformed to account for non-normality.

Measures of tolerance

For 2012-13 data a hyperbolic yield loss curve was used to estimate cultivar tolerance to weed pressure based on weed counts on all plots. All data points were plotted as yield versus *A. myosuroides* density, with the hyperbolic function curve plotted following the formula:

$$Yield = Y_{weedfree} \times \left(\frac{1-i \times D}{(100 \times (1+i \times D/a))} \right) \quad (5)$$

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 calculated as percentage reduction of yield per *A. myosuroides* individual per m².

$$YL = \frac{(100 \times (1 - (Y_{weedy} / Y_{weedfree})))}{D} \quad (6)$$

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.

In order to make two years results comparable, % yield reduction was changed to % of potential yield by subtracting % yield reduction value from 100.

Cultivar traits

Height and stem production was modelled using an unconstrained generalised logistic curve and a split-line model, respectively (see section 3.3.2). 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.

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.

3.4. Relative Weed Green Area model

3.4.1. Experimental design

Cultivars that were present across all three years of experimentation were those. 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.

A total of 320 pots (90 x 90 x 95 mm) were filled with the clay weed loam mixture and arranged in four columns that were 5 pots wide on sand-beds. Each pot was sown by hand with three seeds to a 10 mm depth, and individuals were thinned down to one.

Sampling was done by randomly selecting one plant of each cultivar, removing it from the pot cleaning roots with running water in a fine mesh sieve. Leaves and stems were counted, and plants were dissected into uncurled leaves, green stem (curled, immature leaves included), pale stem and roots. Using the WinDIAS programme, a leaf area and green stem area measured, and leaves, stems and roots were dried at 80°C for a minimum of 18 hours and weighed. These data were used to calculate specific leaf area, leaf area ratio, root weight ratio, aboveground biomass and total biomass. Sowing and harvesting dates for each year are listed in Table 3.3.

Table 3.3 - 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.

Year	Sow date	Harvest number				
		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

Ecophysiological traits for each cultivar were determined from the raw data collected, and calculated. This data underwent Pearson's correlation analysis using Genstat 16, 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.

3.4.2. Acquiring the parameters

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. 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, $\text{g}^{-1} \text{g}^{-1} \text{d}^{-1}$). It may also be applied to area (for example, plant green area).

Table 3.4 - 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)

	$(\text{Ln})L_0$ (cm^2)	RGR_{GA} ($\text{cm}^2 \text{cm}^{-2} \text{tt}^{-1}$)	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

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:

$$\text{Ln}(L) = \text{Ln}(L_0) + \text{RGR} \times \text{tt} \quad (7)$$

$\text{Ln}(L_0)$ 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 3.5:

$$\ln(L_0) + tt \times RGR_{GA} \quad (8)$$

The result can be used to predict stand green area by accounting for the density of plants per m² in equation 9:

$$(\ln(L_0) + tt \times RGR_{GA}) \times D \quad (9)$$

Where D represents the density of the stand (m⁻²). In Figure 3.2, the growth of two virtual plants is presented based on predictions.

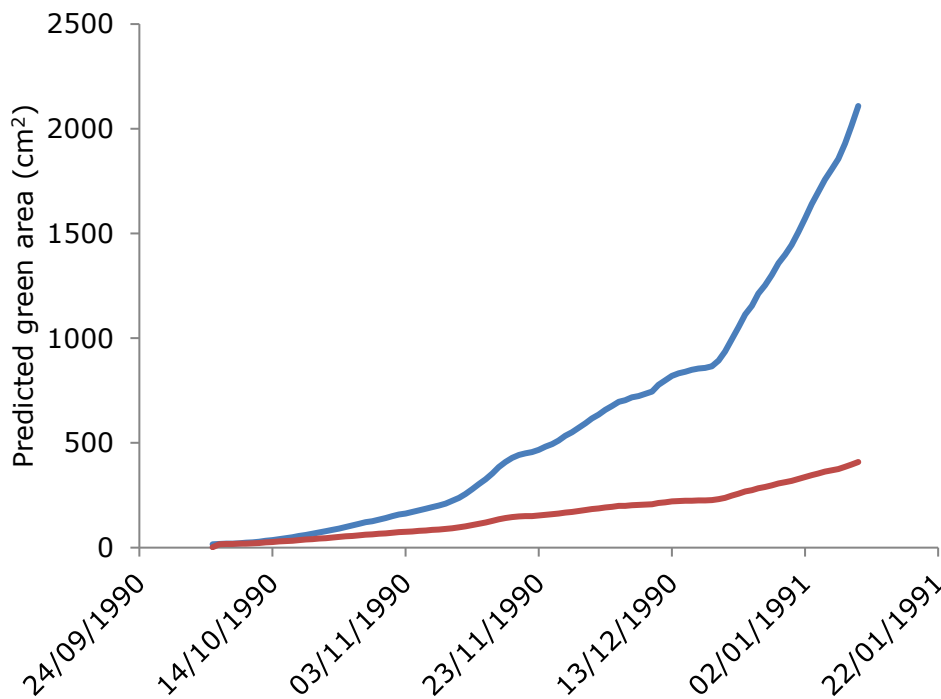


Figure 3.2 - The green area growth of two virtual plants during the exponential phase, as predicted by equation 2.3. Low RGR = Red (0.007 cm² cm⁻² d⁻¹); High RGR = Blue (0.005 cm² cm⁻² tt⁻¹). The difference in the RGR between two competing species will determine the value for G_w input into the RGA model. 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.

3.4.3. 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. 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

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 10.

$$YL = \left(\frac{q G_w}{1 + \left(\frac{q}{m-1}\right) \times \left(\frac{GAI_w}{G_w}\right)} \right) \times 100 \quad (10)$$

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. This result to changes to the predicted GAI_w – a central component to equation 10. 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.

3.5. INTERCOM

Since its initial development, INTERCOM (INTERplant COMpetition) has become one of the most widely used crop-weed competition models. 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. Its use to examine cultivar choice has been limited. 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*. 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).

3.5.1. Sensitivity analysis

Sensitivity analysis was used to identify traits that have important implications for predictions of yield loss and *A. myosuroides* fitness. Numerous wheat traits are included in the model, and those of interest in this study are listed in Table 3.7. 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% 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. It 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.

Table 3.7 - 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
<i>Logistic functions for height</i>			
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

3.5.2. Parameterising the model

Using data acquired from the container experiments, INTERCOM can be parameterised for cultivars, and *in silico* experiments run with the model. The model was parameterised for cultivars Duxford and KWS Santiago, which were the often the strongest and weakest suppressors respectively, 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.

The original parameters for wheat and for the two cultivars can be found in Table 3.7. 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. The phyllochron is not immediately available from experimental data. This 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 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*.

3.5.3. 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.

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 11).

$$Y = a + \frac{b}{(1 + D + x)} \quad (11)$$

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.

4. Results

The temperature across the three years differed, and of particular note is the prolonged cold temperatures into the spring of 2013 (Figure 4.1). In 2011-12, the mean daily temperature was 8.3°C, 6.3°C in 2012-13 and 8.9°C in 2013-14. Rainfall in the field experiment is presented in Figure 4.2.

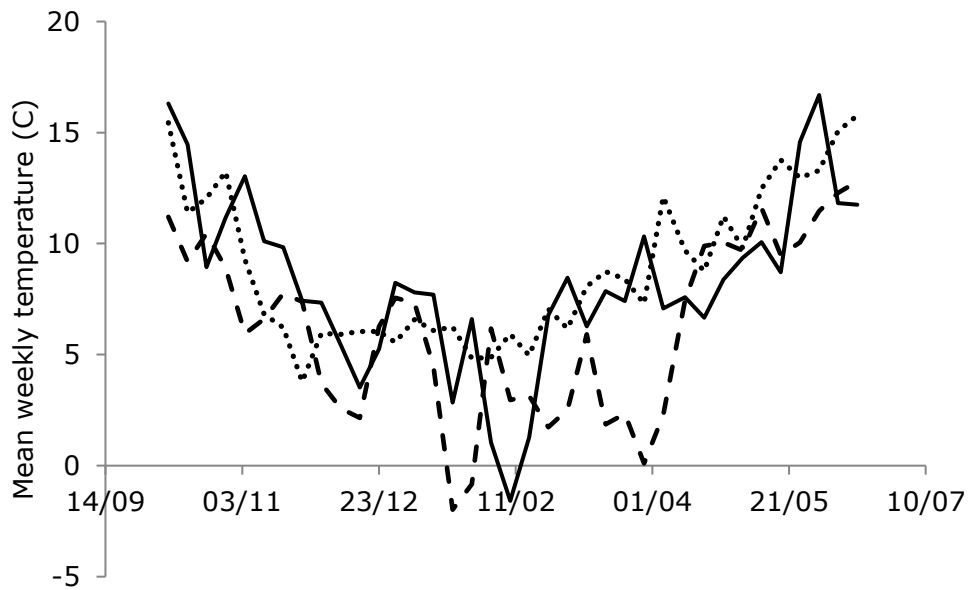


Figure 4.1 - Mean weekly temperatures during experiment at Rothamsted, Herts, UK. Solid line = 2011-12; Dashed line = 2012-13; Dotted line = 2013-14

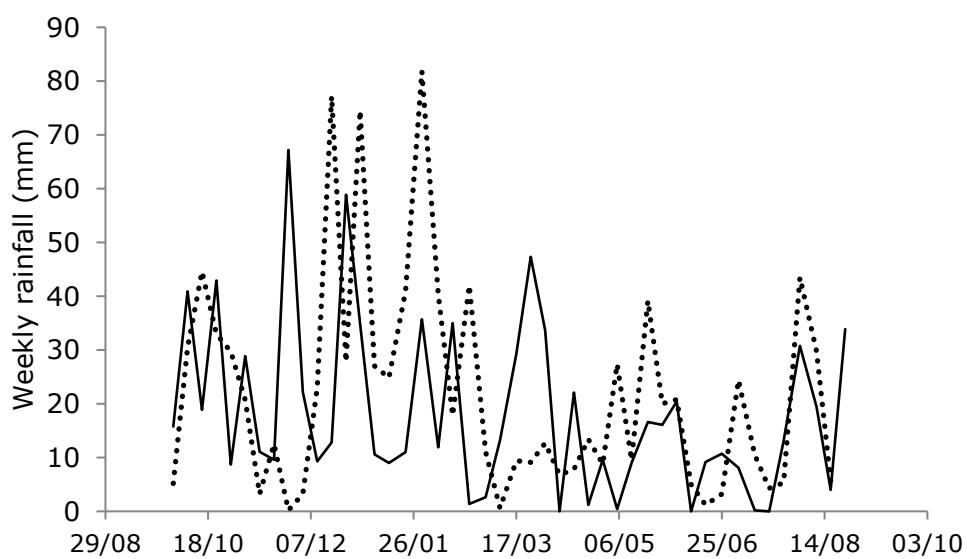


Figure 4.2 - Weekly rainfall at Rothamsted Research, Herts, UK during the experiment. Solid = 2012-13; Dashes = 2013-14

4.1. The sand-beds experiments

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

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 4.3). 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 4.4).

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 and risked strongly influencing data analyses. Many traits were related to the suppressive ability to cultivars, often it was only in a single year (Table 4.1).

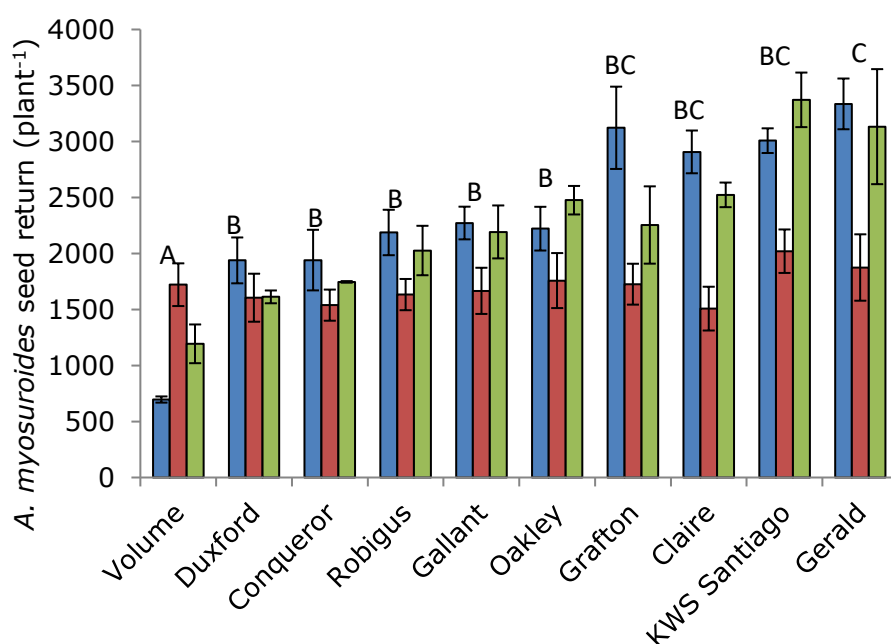


Figure 4.3 - Mean *A. myosuroides* seed return (plant⁻¹) when grown alongside cultivars in different years. All cultivars are wheat, except Volume (barley) and Gerald (oat). Letters denote Bonferroni significance levels. Bars indicate standard error. ■ = 2011-12; ■ = 2012-13; ■ = 2013-14

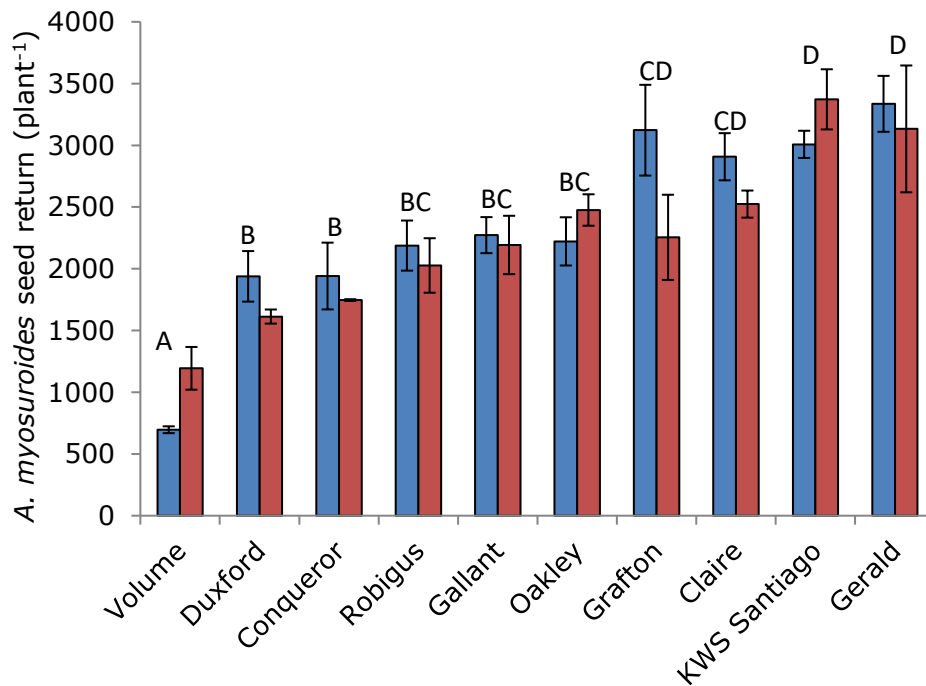


Figure 4.4 - Mean *A. myosuroides* seed return (per plant) when grown alongside cultivars in different years, excluding the atypically cold year of 2012-13. All cultivars are wheat, except Volume (barley) and Gerald (oat). Letters denote Bonferroni significance levels. Bars indicate standard error. ■ = 2011-12; ■ = 2013-14

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 4.5). 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 4.6). The cultivars Duxford and KWS Santiago occupy opposite domains of axis one, reflecting their respective positioning in terms of suppressive ability. 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. 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 4.1 - 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**

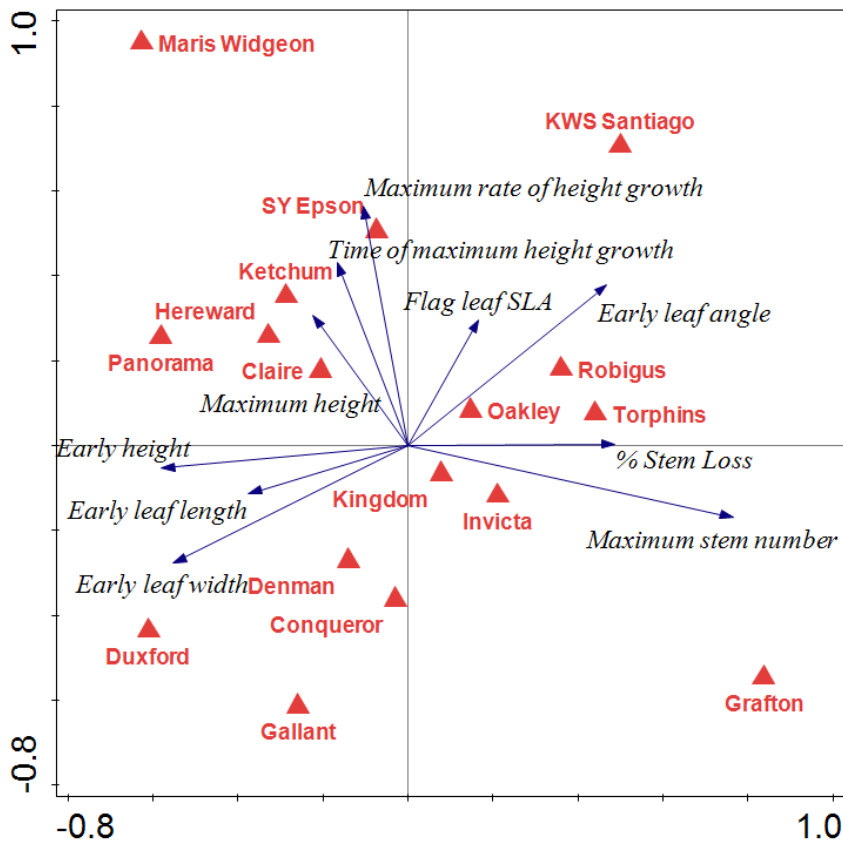


Figure 4.5 - Redundancy analysis ordination plot of wheat traits, with wheat cultivar as the explanatory variable and year as a covariate. Axis one accounts for 19.68% of the variance, and the cumulative variance in 31.24% ($F=1.7$, $P=0.002$). The ten traits with the highest loadings are shown.

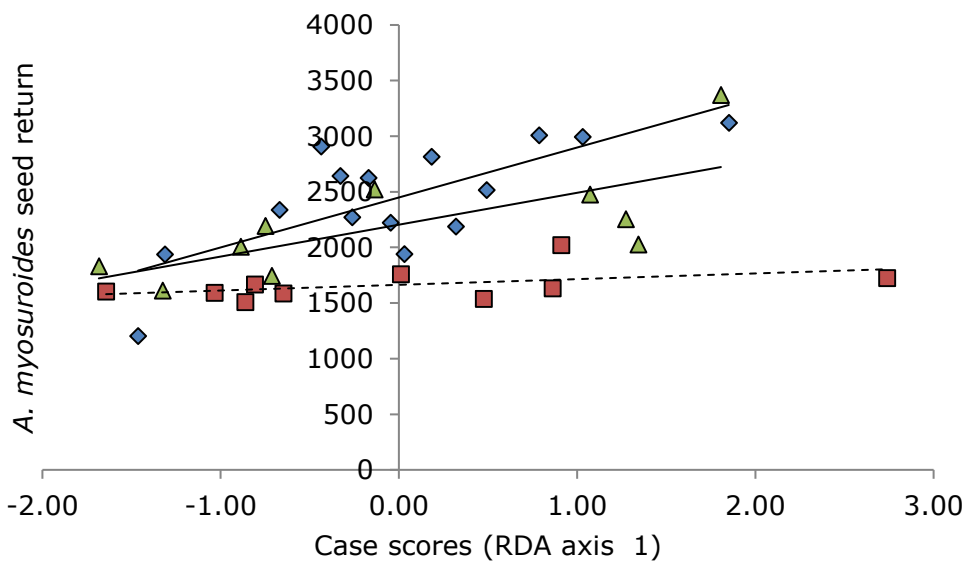


Figure 4.6 - Redundancy analysis case scores (axis one) correlated to seed return over the three experimental years. \blacklozenge = 2011-12 ($P=0.0015$; $r^2=0.7441$), \blacksquare = 2012-13 ($P=0.1954$; $r^2=0.4468$), \blacktriangle = 2013-14 ($P=0.0205$; $r^2=0.7137$).

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 erect leaves) and increased stem retention (Table 4.2). Year was also a strong determinant of *A. myosuroides* seed return, but did not interact with the three significant traits. 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 4.3).

Table 4.2 - 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
<i>Sequentially adding terms to fixed model</i>					
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
<i>Dropping individual terms from full fixed model</i>					
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

Table 4.3 - 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
<i>Sequentially adding terms to fixed model</i>					
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
<i>Dropping individual terms from full fixed model</i>					
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

4.2. The field experiments

Cultivar density was $114.4 \pm 3.45 \text{ m}^2$ in 2012-13, and $281.1 \pm 9.07 \text{ m}^2$ 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 .

There was 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 4.7), but not when measured on the basis of seed return per m^2 (Figure 4.8). 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 ($r=-0.476$; $P=0.1643$).

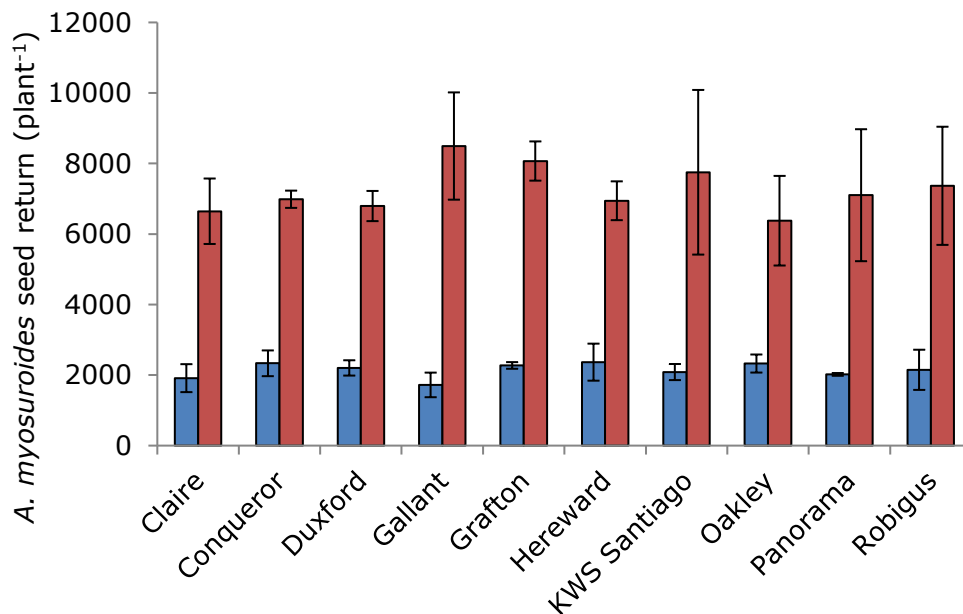


Figure 4.7 - Mean *A. myosuroides* seed return (on a 'per *A. myosuroides* individual' basis) when grown in the field with wheat cultivars in different years. Bars indicate standard error. Blue = 2013-14; Red = 2012-13.

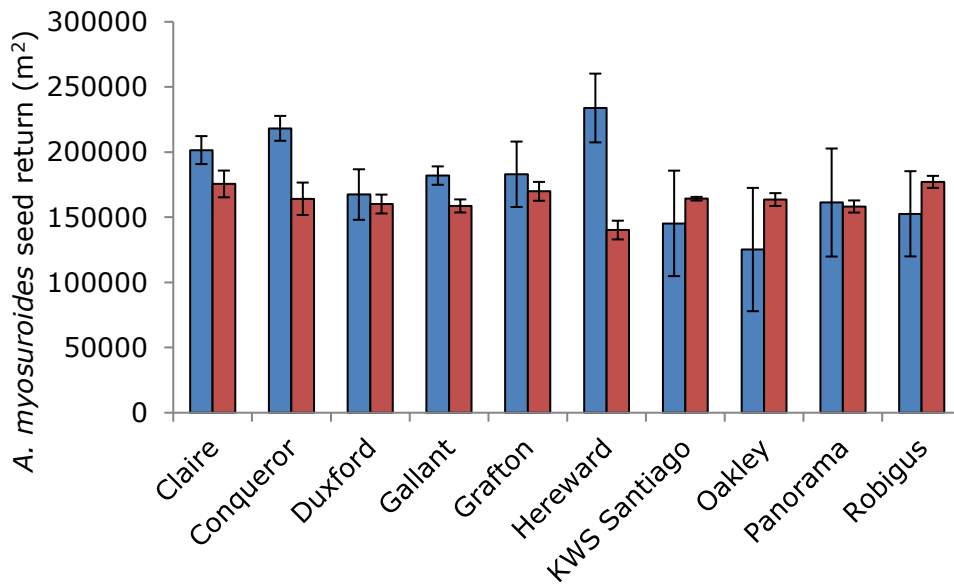


Figure 4.8 - Mean *A. myosuroides* seed return (on a m⁻² basis) when grown in the field with wheat cultivars in different years. Bars indicate standard error. ANOVA detected no differences between cultivars (d.f. 9; P=0.891), year (d.f. 1; P=0.345), nor a cultivar by year interactions (d.f. 9; P=0.686)

It is difficult to compare tolerance ability between the two years due to the different measures used (Figure 4.9 and 4.10). 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 ($r=0.669$; $P=0.024$).

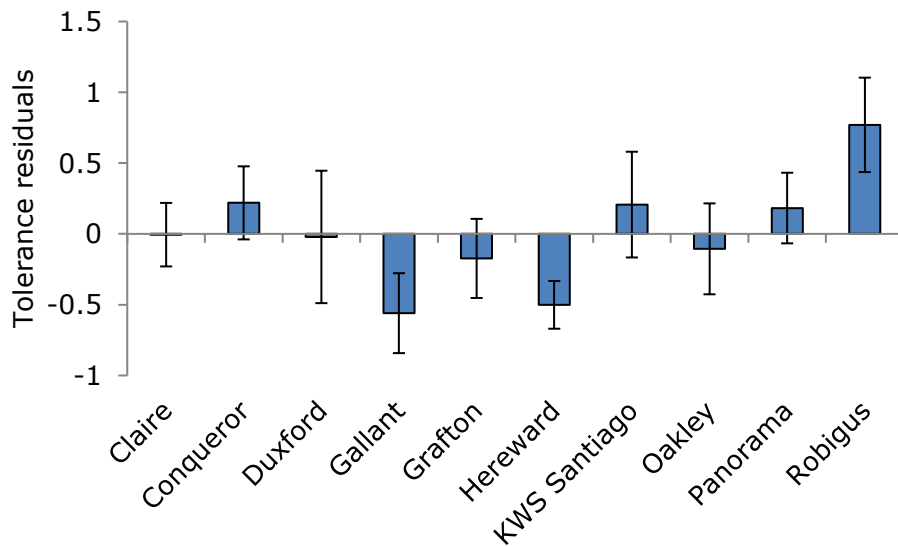


Figure 4.9 - Cultivar tolerance in the 2012-13 experiment, with error bars. (d.f. 9; P=0.175). Cultivar tolerance is represented as the mean bias error of subplot residuals from a rectangular hyperbole of subplot yield and *A. myosuroides* density (see section 0).

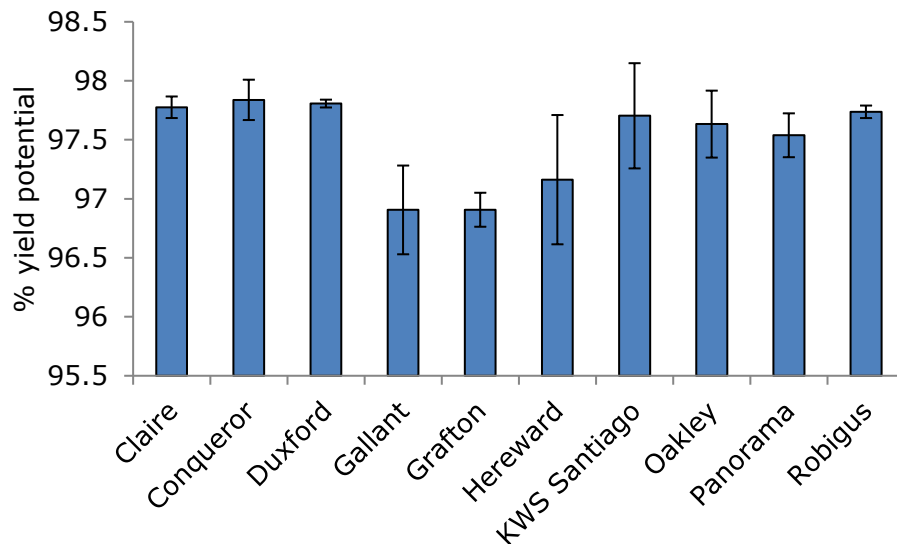


Figure 4.10 - Cultivar tolerance in the 2013-14 experiment, recorded as % of total potential yield under weed pressure, with error bars. (d.f. 9; P=0.678)

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 4.4). These traits have dominated PC1 along with % stem loss, TGW and time of maximum slope in 2012-13 (Figure 4.11 and 4.12). 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.

The REML analysis reported that early leaf number, early leaf area, early green area and ABGW are all predictors of *A. myosuroides* seed production. 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, indicating little value from additional traits. Experimental year was 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*. 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.

In both study years, a relationship between the measures of tolerance and suppressive ability was observed (though weakly in 2012-13) (Figures 4.13 and 4.14). These results imply that in wheat cultivars, good suppressive ability will coincide with ability to resist yield loss caused by *A. myosuroides* pressure.

Table 4.4 - 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 0). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. $N = 30$.

Cultivar traits	Seed return		Tolerance	
	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

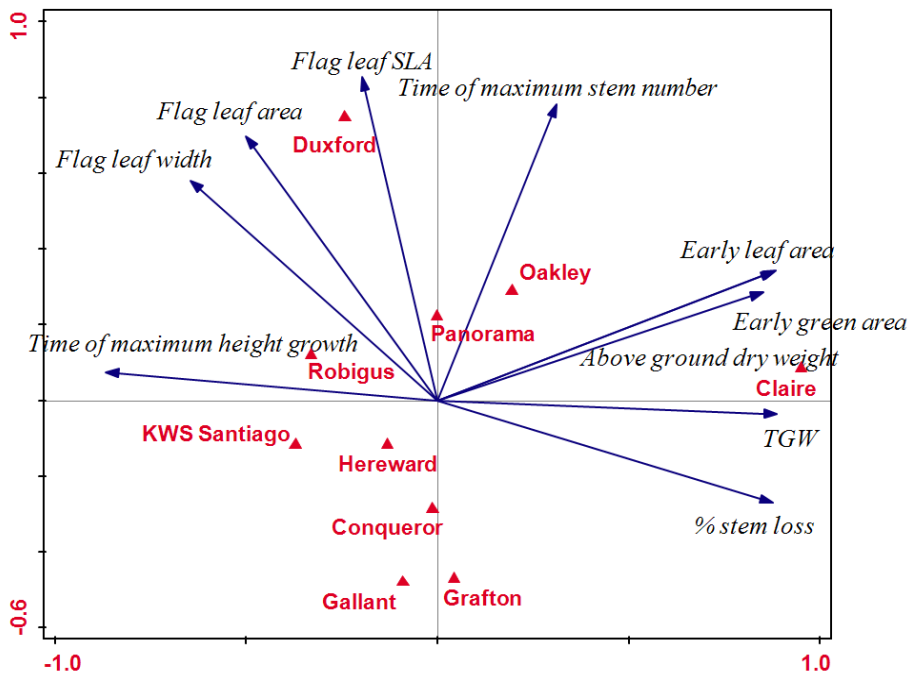


Figure 4.11 - Redundancy analysis ordination plot of wheat traits for the 2012-13 experiment, with wheat cultivar as the explanatory variable. Axis one accounts for 34.83% of the variance, and the cumulative variance in 62.44%. The ten traits with the highest loadings are shown.

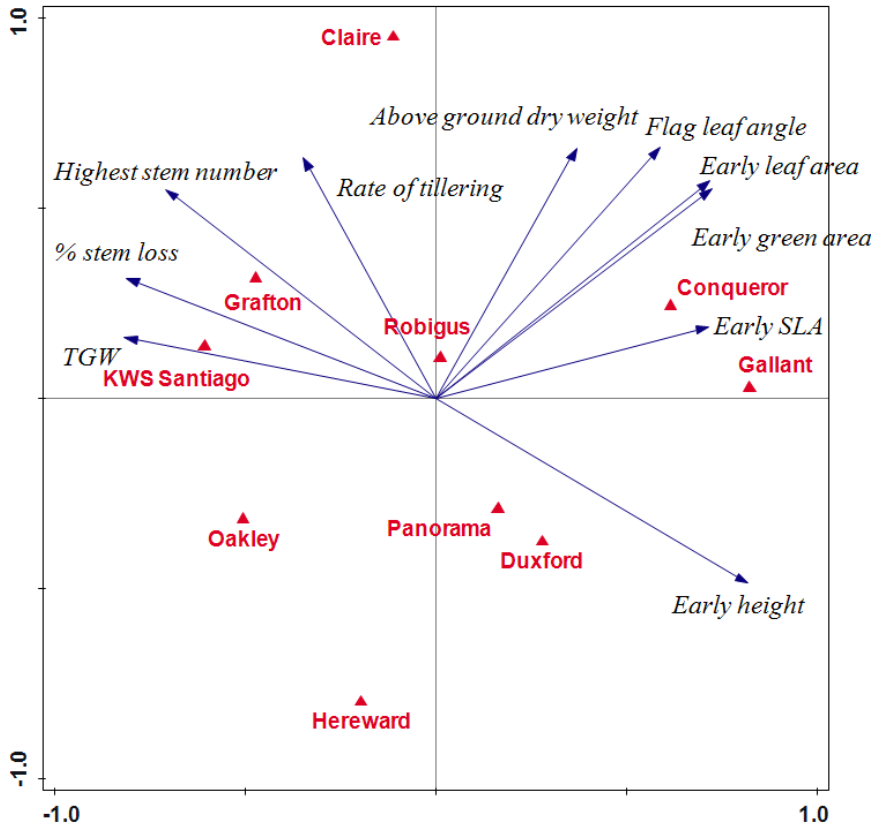


Figure 4.12 - Redundancy analysis ordination plot of wheat traits for the 2013-14 experiment, with wheat cultivar as the explanatory variable. Axis one accounts for 27.15% of the variance, and the cumulative variance in 46.89%. The 10 traits with the highest loadings are shown.

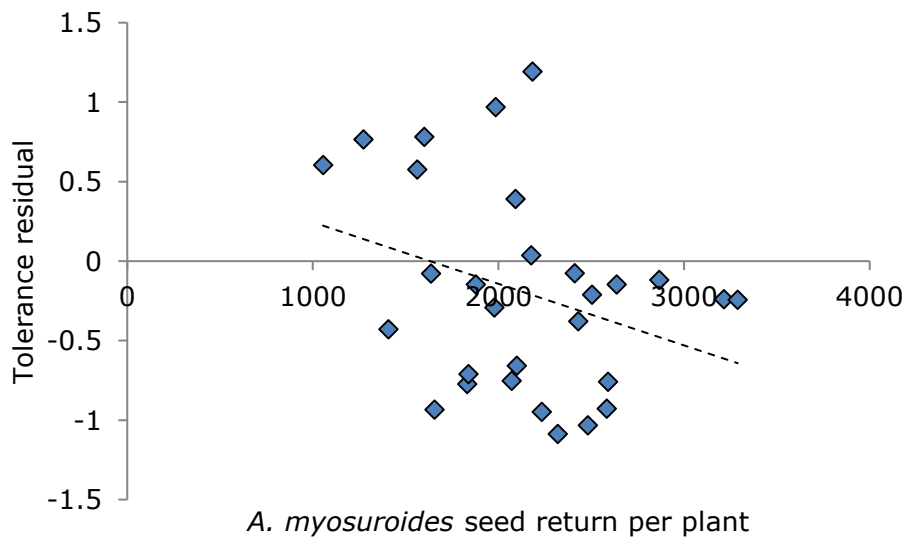


Figure 4.13 – The relationship between tolerance and suppressive ability in 2012-13 (N=30; P=0.0879, $r = -0.3225$)

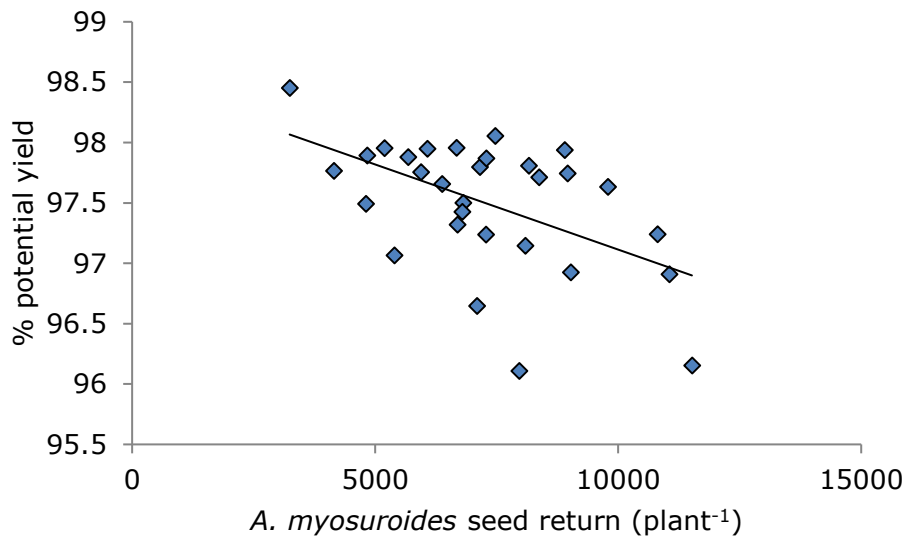


Figure 4.14 - The relationship between tolerance and suppressive ability in 2013-14 (N=29; P=0.0032, $r = -0.5199$)

4.3. Relative weed green area model

Predictions of yield loss differed between cultivars (Figure 4.15).

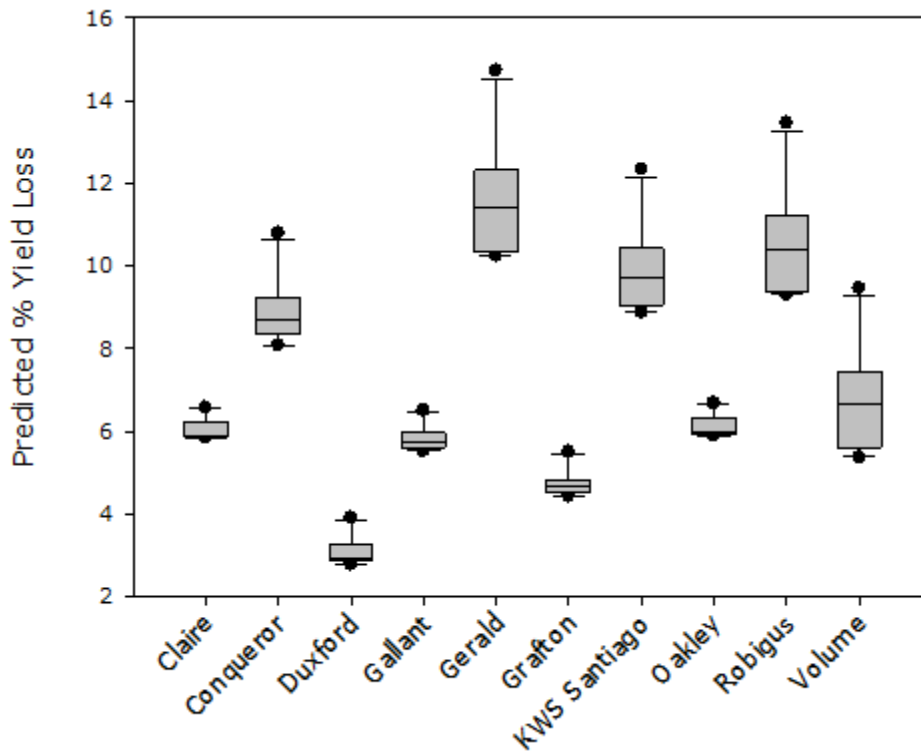


Figure 4.15 - The predicted yield loss (%) for each cultivar for years 1990-1999. All cultivars are wheat except Gerald (oat) and Volume (barley)

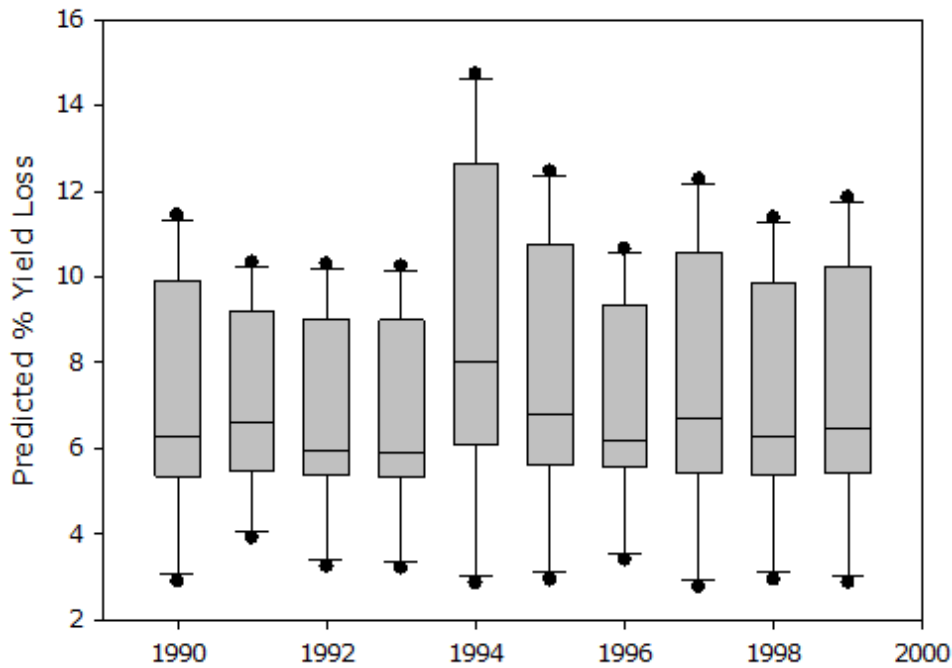


Figure 4.16 - Predicted yield loss (%) during the years 1990-1999. All cultivar values included.

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 over the ten years (Figure 4.16) 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 4.17 and 4.18). 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, it always had a lower predicted green area than the cultivars modelled. This can be attributed to lower L_0 values for *A. myosuroides*.

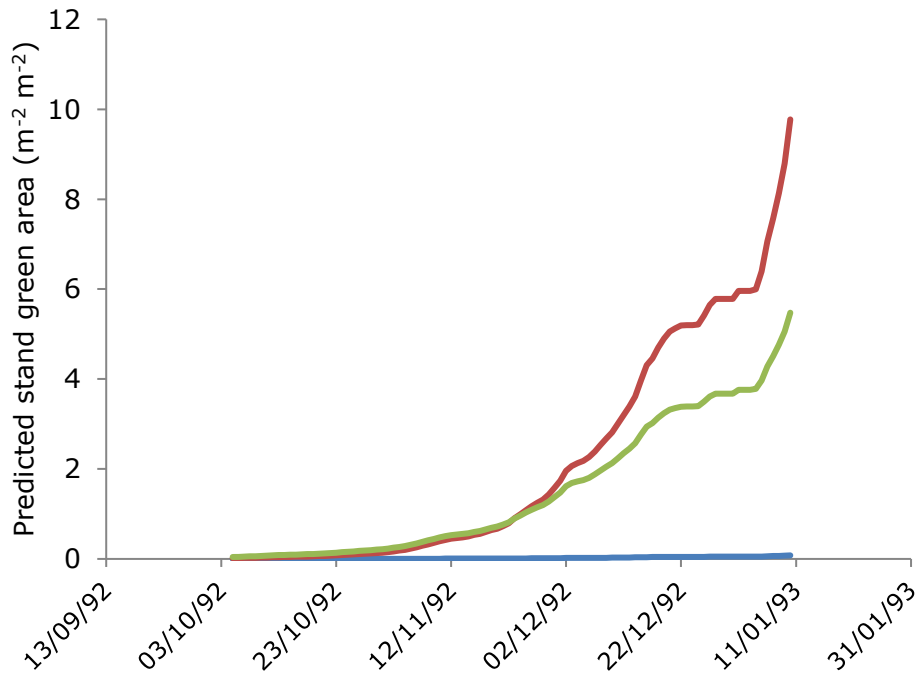


Figure 4.17 - The predicted green area growth of *A. myosuroides* and the highest (Duxford) and lowest (Volume) RGR-ranked cultivars, according to 1992/93 thermal time data (average air temperature 5.68°C). Cultivar density 186 m⁻², *A. myosuroides* density 20 m⁻². Blue = *A. myosuroides*; Red = Duxford; Green = Volume.

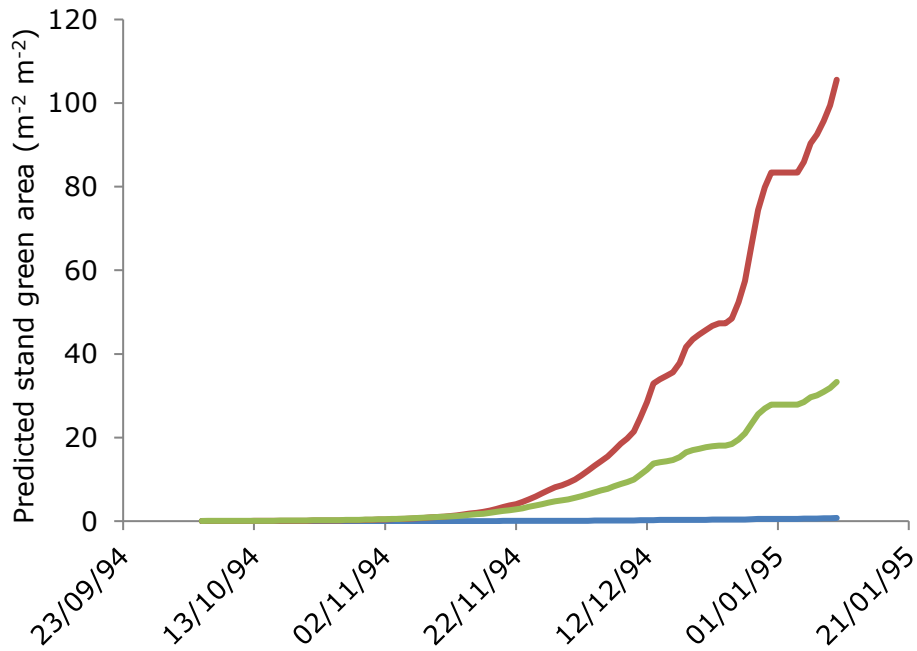


Figure 4.18 - The predicted green area growth of *A. myosuroides* and the highest (Duxford) and lowest (Volume) RGR-ranked cultivars, according to 1994/5 thermal time data (average air temperature 8°C). Cultivar density 186 m⁻², *A. myosuroides* density 20 m⁻². Blue = *A. myosuroides*; Red = Duxford; Green = Volume.

4.4. INTERCOM model

4.4.1. Sensitivity analysis

Figure 4.19 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%.

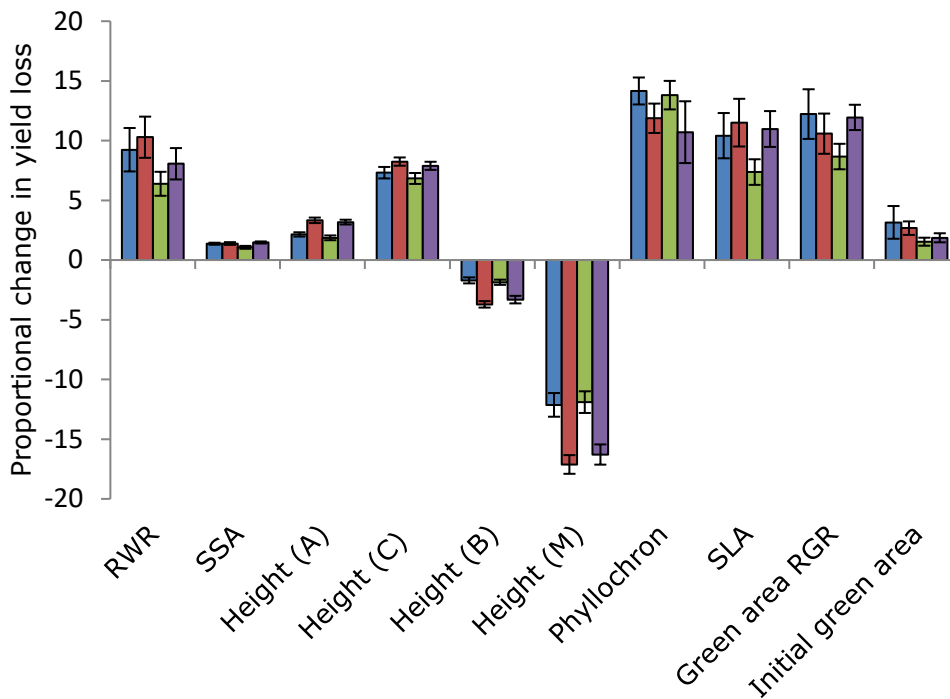


Figure 4.19 - The mean proportional change in % yield loss when INTERCOM parameter traits are decreased in value by 5%. Simulation model was run with weather data from 2005-2014. ■ = 300 plants m⁻² sown 20 Sept; ■ = 300 plants m⁻² sown 20 Oct; ■ = 150 plants m⁻² sown 20 Sept; ■ = 150 plants m⁻² sown 20 Oct. Bars indicate standard error.

4.4.2. Cultivar competitive ability

By parameterising the model for Duxford and KWS Santiago, we see that the cultivars maintain the same suppressive ranking as were seen in the sand-beds experiment (Figures 4.20 and 4.21). 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.

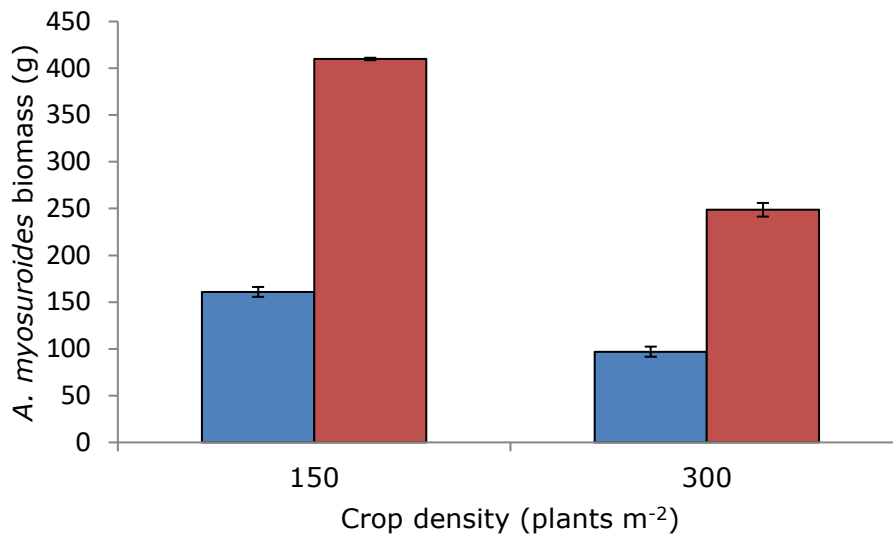


Figure 4.20 - The INTERCOM predictions of *A. myosuroides* seed return when grown with cultivars Duxford and KWS Santiago at different crop densities. The model was run using weather data from 2005-2014. Sowing date 20 September. ■ = Duxford; ■ = KWS Santiago

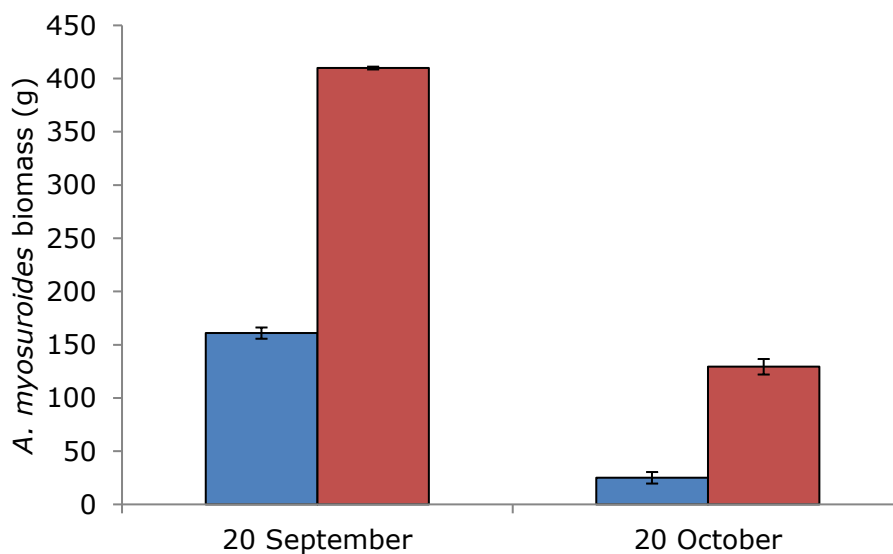


Figure 4.21 - The INTERCOM predictions of *A. myosuroides* seed return when grown with cultivars Duxford and KWS Santiago at different sowing dates. The model was run using weather data from 2005-2014. Crop density 150 plants m². ■ = Duxford; ■ = KWS Santiago

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. 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 4.22). The impact

of sowing date has a similar effect, with Duxford consistently more competitive than KWS Santiago (Figure 4.23). 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.

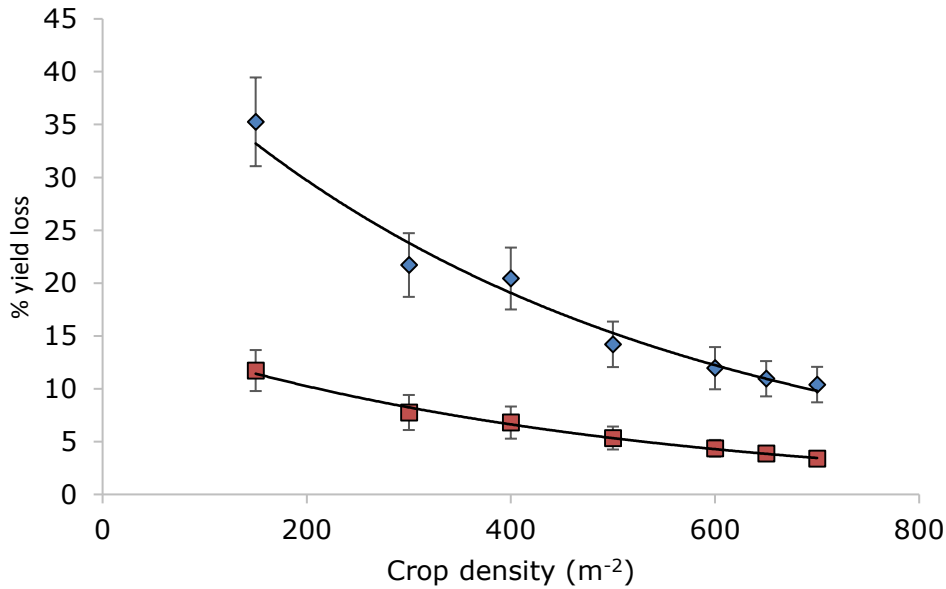


Figure 4.22 - The % yield loss predictions of cultivars when sown at different densities, with *A. myosuroides* at 80 plants m⁻². Sowing date 20 September. Bars denoted standard error. ♦ = KWS Santiago ■ = Duxford

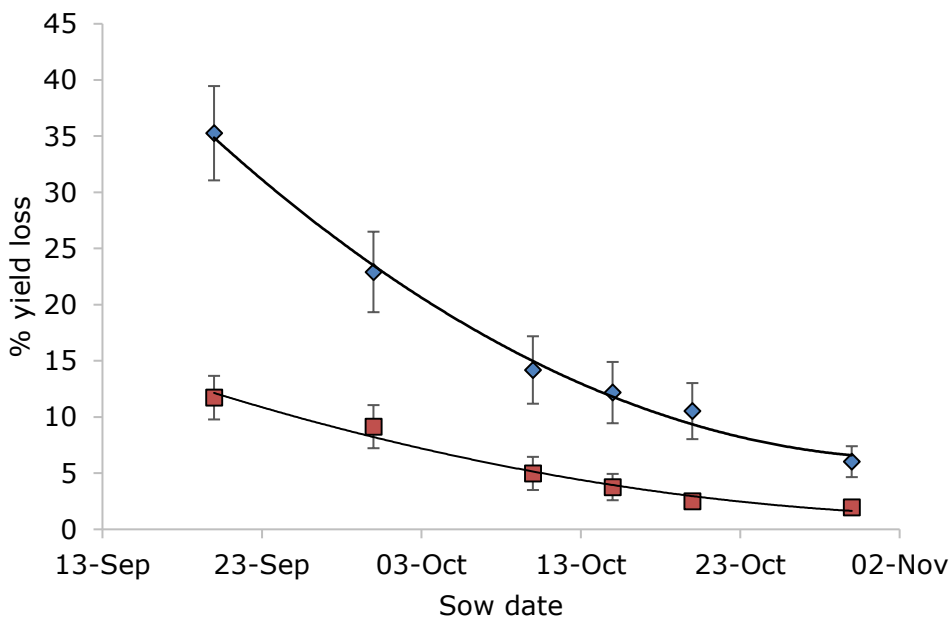


Figure 4.23 - The % yield loss predictions of cultivars when sown at different dates. Crop density 150 plants m⁻², *A. myosuroides* density 80 plants m⁻². Bars indicate standard error. ♦ = KWS Santiago ■ = Duxford

5. Discussion

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 stems. 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 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).

5.1. Early vigour traits

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 (Weaver *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.

5.2. Development traits

Traits associated with later stages of development were also related to *A. myosuroides* seed return. Faster spike emergence and lower maximum stem 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 (reduced % stem loss was 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 stems 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. 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.

5.3. Interaction between competitive traits and environmental conditions

No traits were associated with suppressive ability in the same way across all studies. 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).

Increased early aboveground weight and green area were important for suppressive ability were important in the containers, 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. 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. However, these are speculations in need of further research.

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 had the greatest differences in traits such as early height and green area. 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.

5.4. Tolerance traits in wheat

No trait could be related to tolerance across study years. 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. 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. However, no trait was related to tolerance and suppression in the same experimental year.

Wang *et al.* (2010) also suggested that ‘tolerance to weed competition’ does not exist and are instead ‘stress-resistance’ traits. 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.

5.5. 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.

5.6. 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). The results of this study confirm 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 a single experiment.

In this report, 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 stem production and loss dynamics under different scenarios would have value.

5.7. 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. Simple measures of leaf number, length and width may sufficiently capture green area. However, the uncertainty surrounding early aboveground weight and early green area presents problems for using these, or derivatives of these, as indicator traits.

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 could be a surrogate for time of spike emergence.

5.8. 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. There was no evidence of a trade-off between suppressive ability and weed-free yield in this study, but since weed-free yield could only be examined in one experiment, a potential trade-off cannot be dismissed.

5.9. Conclusions

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

6. References

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