

Using simulation models to investigate the cumulative effects of sowing rate, sowing date and cultivar choice on weed competition

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1 **Using simulation models to investigate the cumulative effects of sowing rate, sowing**
2 **date and cultivar choice on weed competition.**

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4

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8

9 **Abstract:**

10 With the increasing pressure on crop production from the evolution of herbicide resistance,
11 farmers are increasingly adopting Integrated Weed Management (IWM) strategies to augment
12 their weed control. These include measures to increase the competitiveness of the crop
13 canopy such as increased sowing rate and the use of more competitive cultivars. While there
14 are data on the relative impact of these non-chemical weed control methods assessed in
15 isolation, there is uncertainty about their combined contribution, which may be hindering
16 their adoption. In this article, the INTERCOM simulation model of crop / weed competition
17 was used to examine the combined impact of crop density, sowing date and cultivar choice on
18 the outcomes of competition between wheat (*Triticum aestivum*) and *Alopecurus*
19 *myosuroides*. *Alopecurus myosuroides* is a problematic weed of cereal crops in North-
20 Western Europe and the primary target for IWM in the UK because it has evolved resistance
21 to a range of herbicides. The model was parameterised for two cultivars with contrasting
22 competitive ability, and simulations run across 10 years at different crop densities and two
23 sowing dates. The results suggest that sowing date, sowing density and cultivar choice largely
24 work in a complementary fashion, allowing enhanced competitive ability against weeds when
25 used in combination. However, the relative benefit of choosing a more competitive cultivar
26 decreases at later sowing dates and higher crop densities. Modelling approaches could be
27 further employed to examine the effectiveness of IWM, reducing the need for more expensive
28 and cumbersome long-term *in situ* experimentation.

29 **Key words:** competition, cultural weed control, INTERCOM, suppression, tolerance

30

31 **1. Introduction**

32 In agricultural systems, a careful balance is required between producing a high value crop
33 yield and minimising costs. In this regard, weeds are the most serious potential threat to
34 maintaining profitable farming systems, responsible for inflicting approximately 34%
35 potential yield loss globally (Oerke, 2006). The introduction of herbicides in the 1960s
36 allowed effective and relatively cheap control of weed species. Unfortunately, over-reliance
37 on herbicides has led to widespread resistance in many problematic weed species (Heap
38 1997; Moss *et al.*, 2011) and the current herbicide-based weed control paradigm is widely
39 considered to be unsustainable. In response, an approach which combines herbicides with a
40 range of non-chemical (or ‘cultural’) weed management options, termed Integrated Weed
41 Management (IWM), is increasingly being employed to compensate for loss of herbicide
42 efficacy (Bond and Grundy 2001; Lutman *et al.*, 2013; Andrew *et al.*, 2015).

43 Non-chemical control techniques employed in IWM are numerous and can be divided into
44 those implemented over several seasons, including rotational ploughing and increased crop
45 diversity, and within-season measures. The latter include increased sowing rate and growing
46 more competitive cultivars to minimise weed seed return. Within-season options, that aim to
47 shift the competitive balance in favour of the crop, are the focus of this paper. In most
48 systems, non-chemical weed management options will be employed in combination with
49 herbicides but by increasing crop competitiveness, the required efficacy and reliance on
50 herbicide control is reduced. In the UK, non-chemical techniques are increasingly being
51 utilised to enhance control of the weed species *Alopecurus myosuroides* Huds. in winter
52 wheat (*Triticum aestivum* L). This annual grass species can cause substantial losses to wheat
53 (Storkey *et al.*, 2003) and herbicide resistance is widespread in North-West Europe (Moss *et*
54 *al.*, 2011; Lutman *et al.*, 2013; Keshtkar *et al.*, 2015), and is the focus of this study.

55 Non-chemical control tools require financial or temporal investments and their effectiveness
56 varies from year to year. The resulting uncertainty means non-chemical control strategies
57 tend only to be utilised when herbicides begin to fail (Bastiaans *et al.*, 2008), as is currently
58 the case for the control of *A.myosuroides* in the UK. Recommended non-chemical control
59 options for *A. myosuroides* in the UK include rotational ploughing, use of spring crops (*A.*
60 *myosuroides* mainly germinates in the autumn), delayed sowing date (to allow the use of a
61 stale seedbed), increased crop sowing rate and the use of more competitive crop cultivars
62 (Lutman *et al.*, 2012).

63 Non-chemical control techniques are infrequently studied in combination, owing to the scale
64 of experiment required, and data are therefore lacking on whether combined effects are
65 additive, synergistic or antagonistic. Weed control measures have previously been examined
66 with the use of simulation models. Models allow a means of studying scenarios *in silico*,
67 providing insight without the need for large-scale experimentation. One well developed and
68 validated model of crop / weed competition is INTERCOM, initially developed by Kropff
69 and Spitters (1992) which has been parameterised for several crop and weed species since its
70 inception (van Ittersum *et al.*, 2003). When tested using sugar beet and *Chenopodium album*
71 L., the original model explained 98% of the variation in yield loss (Kropff *et al.*, 1992) and
72 since then has been adapted to model competition from a range of weed species, including
73 *A.myosuroides* in winter wheat under UK conditions (Storkey & Cussans, 2007). The model
74 includes a range of eco-physiological parameters that determine the competitive balance
75 between crops and different weed species and is weather driven allowing variability in output
76 owing to environmental stochasticity to be quantified. The model can be used to examine the
77 impact of sowing density, sowing date and crop cultivar on the outcome of crop / weed
78 competition.

79 In this paper, we demonstrate how the INTERCOM model of plant competition can be
80 utilised to observe the combined effect of sowing density, sowing date and cultivar choice,
81 using wheat and *A. myosuroides* as model species. Furthermore, we discuss the advantages
82 and disadvantages in employing models to understanding weed control initiatives and
83 advising on their future use to support the implementation of IWM.

84 **2. Materials and methods**

85 **2.1. Description of the *INTERCOM* model**

86 The INTERCOM model makes predictions of the outcomes of competition between a crop
87 and a weed based on leaf area production and distribution through the canopy in daily time
88 steps (Kropff & van Laar, 1993). The primary driving environmental variables are
89 photoperiod, temperature and available water. Temperature and water are growth-limiting,
90 whilst accumulated photoperiod and thermal time mediate switches between developmental
91 stages. The model has three discrete periods. Before plants begin competing for resources,
92 growth is sink limited and modelled using an exponential relationship with biological time. In
93 the original model, thermal time was used but, in later versions, a variable incorporating
94 incident radiation (effective day degrees) was found to better capture differences between the
95 growth of autumn and spring emerging cohorts (Storkey, 2004). A total green area index
96 (GAI) of 0.75 is used as a switch between sink and source limiting growth – the next phase of
97 the model. The ability of crop and weed to intercept light is determined through their share of
98 the canopy (leaf area index), leaf traits related to light absorption (such as specific leaf area)
99 and the vertical distribution of leaf area through the canopy. The model also accounts for
100 changes in leaf traits and light absorption over time (Storkey, 2005). Plant height growth is
101 predicted to follow the logistic function against accumulated photothermal time, as defined
102 by Spitters (1989). Precipitation data and soil water balance functions are included in the

103 model, using calculated rates of transpiration and evaporation. Water becomes limiting when
104 soil moisture falls below a pre-determined level, and the relationship between the potential
105 growth rate and water limited growth determined from an empirically derived relationship
106 The final phase of the model is senescence and, for wheat, grain filling. Re-allocation of
107 resource from stems and leaves to grain is modelled using functions from the Sirius model of
108 wheat growth (Jamieson *et al.*, 1998).

109 The version of INTERCOM utilised in this study has been parameterised for winter-sown
110 wheat and *A. myosuroides* for improved description of winter wheat growth and partitioning
111 (see Storkey & Cussans, 2007, where a detailed description of the model can be found). It
112 was amended for the purposes of this study in C++ as described below.

113 ***2.2. Parameterising INTERCOM for wheat cultivars***

114 In the winter wheat / *A. myosuroides* model, wheat was originally parameterised using data
115 from the cultivar Consort (Storkey & Cussans, 2007). However, it has been frequently
116 demonstrated that wheat cultivars differ in their ability to compete against weeds. While
117 INTERCOM has been used in the past to inform the breeding of competitive rice cultivars
118 (Bastiaans *et al.*, 1997), here, we take the novel approach of using the model to quantify the
119 relative impact of cultivar choice on weed competition in the context of variable sowing rate
120 and sowing date. The variability in cultivar competitive ability has been attributed to
121 numerous plant traits, including height, leaf area and developmental speed (Andrew *et al.*,
122 2015). Many of these are traits utilised by INTERCOM to make predictions of competitive
123 outcomes.

124 The model was parameterised for two contrasting wheat cultivars, Duxford and KWS
125 Santiago. These cultivars were selected based on three years of study (2012, 2013, 2014) in
126 outdoors containers, where they represented the extremes in terms of competitiveness when

127 compared to a range of ten modern wheat cultivars. Duxford was frequently reported as the
128 strongest suppressor of *A. myosuroides* across three years of study, whilst KWS Santiago was
129 frequently the poorest performer (Andrew, 2016). Using data collected from a series of
130 outdoor, container-based experiments based at Rothamsted Research, UK, data were
131 available to parameterise the model for different cultivars. To parameterise seedling growth
132 rate, the protocol used in Storkey (2004) was followed; sequentially sampling seedlings over
133 a two month period. For parameters determining resource competition, the cultivars were
134 grown in competition with *A. myosuroides* in outdoor containers (40 x 32 cm) in a fully
135 replicated experimental design repeated over three years and a range of morphological traits
136 measured through the season. A selection of the original model parameters for wheat (cv.
137 Consort) and for the two contrasting cultivars can be found in Table 1. The model was
138 separately parameterised for each cultivar in C++. The main differences between the cultivars
139 were in their rate of development, early height and early vigour (Figure 1). Duxford tended to
140 have a relatively erect canopy structure early on and a high seedling growth rate (related to a
141 higher specific leaf area and lower partitioning to roots) whereas KWS Santiago tended to
142 delay shoot extension and be relatively prostrate in the seedling stage.

143 *Table 1 and figure 1 near here*

144 **2.3. Simulations**

145 A number of *in silico* experiments were done using INTERCOM. Firstly, data input for
146 INTERCOM can be amended to reflect the density of wheat and *A. myosuroides* in the stand
147 and wheat sowing date; the interaction of these two factors was analysed using the original
148 parameters for the cultivar, Consort. Crop densities between 100 and 400 wheat plants m⁻²
149 were selected to represent the potential to increase the competitive ability of the wheat
150 canopy with *A. myosuroides* without changing cultivar choice. A range of sowing dates was

151 chosen to reflect a realistic period for sowing winter wheat in the UK (15 September – 14
152 November). Emergence times after sowing were kept constant at seven days for *A.*
153 *myosuroides* and 10 days for wheat, and the *A. myosuroides* density was maintained at 80
154 plants m⁻² across all simulations. To quantify the interaction of sowing date and sowing rate
155 on crop canopy competitiveness, the model was run using 49 combinations of rate x date,
156 using intervals of 50 plants m⁻² for crop density and 10 days for sowing date. The simulation
157 model was run using radiation, temperature and precipitation data recorded at Rothamsted
158 meteorological station for harvest years 2005-2014, providing yearly predictions of
159 percentage crop yield loss and *A. myosuroides* above-ground dry weight (m⁻²).

160 The second experiment analysed the differences between the cultivars, Duxford and KWS
161 Santiago, at a range of crop densities (this time increased to a maximum of 600 plants m⁻²)
162 and a similar range of sowing dates as the first experiment. The ten years of weather data
163 were used and the mean and standard error for crop yield loss calculated for each
164 combination of cultivar x crop density or cultivar x sowing date. Finally, the effect of
165 variable weather was made the focus of a further analysis, using a small number of cultivar x
166 sowing date x crop density scenarios. A preferred sowing date under weed-free scenarios (20
167 September) was chosen along with a later sowing date, utilised to reduce *A. myosuroides*
168 competitive ability and its germination within the crop competitive ability (20 October)
169 (Melander, 1995; Lutman *et al.*, 2013). Two realistic crop densities were also chosen, 150 or
170 300 plants m⁻². Each combination of sowing date and crop density was input into
171 INTERCOM using the parameters for either Duxford or KWS Santiago using weather data
172 from each of the ten years. We assumed that the yearly weather data are temporally
173 independent which allowed the differences between the cultivars, sowing dates or drilling
174 dates (and interactions between them) to be analysed in the context of this inter-annual

175 environmental variability using ANOVA. All statistical analysis of data was conducted in
176 Genstat 16 (VSN International, 2013).

177 **3. Results**

178 In the model's predictions, percentage yield loss and *A. myosuroides* biomass at maturity
179 were closely correlated ($r = 0.86$; $P < 0.001$). As such, although percentage yield loss is
180 presented, the model predicted an equivalent reduction in weed biomass. In addition, the
181 relationship between *A. myosuroides* biomass at maturity and seed production is observed to
182 be positively correlated, allowing the output to be used to predict seed return under different
183 scenarios. An increase of 10% yield loss was associated with approximately 15000 additional
184 weed seeds produced. When using parameters for a standard cultivar, Consort, the model
185 predicted decreasing yield loss with both increasing crop density and a later sowing date; in
186 both cases the relationship was non-linear (Figure 2).

187 *Figure 2 near here*

188 Higher yield loss was always observed for KWS Santiago ($F_{1,76}=34.33$, $P < 0.001$), regardless
189 of crop density or sowing date. However, yield loss varied for both cultivars across the
190 different seasons and the relative difference between the cultivars was highly weather
191 dependent (Figure 3a). These predictions are in line with empirical observations of weed
192 suppression from the container experiments used to parameterise the model for Duxford and
193 KWS Santiago (Figure 4).

194 *Figure 3 & 4 near here*

195

196

197 Accumulated thermal time was an important determinant of yield loss predictions in the
198 INTERCOM model for both cultivars, with lower temperatures resulting in decreased yield
199 loss ($F_{1,76}=21.62$, $P<0.001$) and reduced differences between the cultivars. In the coldest year,
200 2013, the model reported the lowest yield loss prediction of 3.2%, whilst the second highest
201 was in the warmest year (2006), with 17% yield loss. The predicted weed-free yield of wheat
202 suffered no equivalent detriment in the colder years (Figure 3b), implying that temperature
203 has a stronger impact on *A. myosuroides* competitive performance.

204 *Figure 5 near here*

205 Percentage yield loss at a crop density of 150 plants m^{-2} averaged 15%, decreasing to 9.4%
206 when crop density was increased to 300 plants m^{-2} ($P = 0.01$; 1 d.f.). Delaying sowing by 30
207 days also reduced percentage yield loss, with 19.1% yield loss on 20 September sowing dates
208 and 5.3% yield loss when the crop was sown on 20 October ($P<0.001$; 1 d.f.) (Table 2).

209 The INTERCOM model predicts that Duxford is the most competitive cultivar across all
210 simulation years, with KWS Santiago suffering 18.5% yield loss whilst Duxford only
211 suffered 5.89% yield loss ($P<0.001$; 1 d.f.) (Table 2). There was no significant interaction
212 between sowing date, sowing density and cultivar choice, suggesting they behave
213 cumulatively when employed together to reduce percentage yield loss.

214 The effects of changing crop cultivar, sowing density and sowing date on weed-free yield
215 was restricted only to sowing date, with delayed sowing resulting in a mean decrease in yield
216 from 13.56 $t\ ha^{-1}$ to 12.79 $t\ ha^{-1}$ ($P<0.002$; d.f. 1) (Table 3).

217 *Table 2 & table 3 near here*

218 The model anticipates Duxford to outperform KWS Santiago at all densities, and the benefit
219 of increased sowing density reduces with each subsequent increase (Figure 5a). In order for

220 KWS Santiago to achieve a similar yield loss to Duxford when sown at 150 plants m⁻² (mean
221 percentage yield loss of 11.7), its stand density must be increased to 640 plants m⁻² (Figure
222 5a). A similar effect is observed with sowing date, with Duxford consistently more
223 competitive than KWS Santiago and the benefit of delayed sowing is reduced with each
224 additional day (Figure 5b). In order for KWS Santiago to achieve a similar yield loss as
225 Duxford sown at 150 plants m⁻² on 20 September, it must be sown on 16 October. However,
226 as sowing density increased or sowing date was delayed, the relative benefit of using a
227 competitive cultivar decreased.

228 *Figure 5 near here*

229 **4. Discussion**

230 There are various non-chemical control strategies available to farmers, and these are often
231 utilised in IWM. However, there is a need to understand how they perform in combination
232 and how they interact with variable weather in order to maximise weed control and minimise
233 yield loss (Barzman *et al.*, 2015). The necessary field experiments to investigate this would
234 require a scale (temporal and spatial) that would make them difficult to conduct and
235 complicated to analyse. The use of simulation models such as INTERCOM can provide
236 valuable insight into their combined effect on crop-weed competitive interactions (van
237 Ittersum *et al.*, 2003).

238 The predictions of the reduction in yield loss with increasing crop density were in agreement
239 with the published literature (Mennan and Zandstra, 2005). The model predicted an average
240 reduction in seed production of 25% when crop density was increased from 100 to 300 plant
241 m⁻². This is an equivalent increase in crop competitiveness as was reported in Lutman *et al.*
242 (2013) where these treatments resulted in reductions in *A. myosuroides* head density of
243 approximately 32%.

244 A similar comparison cannot be made with data from Lutman *et al.* (2013) on the impact of
245 delayed sowing on weed competition as we did not incorporate the effect of reduced weed
246 establishment at late sowing dates. This would be a useful improvement of the models.
247 However, the model output was realistic in that it predicted that in the wheat – *A.*
248 *myosuroides* scenario, the crop acquires a competitive advantage when sown at higher
249 densities and at later sowing dates. The benefit of increased sowing density has been
250 observed in various crop-weed associations (Christensen *et al.*, 1994; Melander, 1995; Cosser
251 *et al.*, 1997; Roberts *et al.*, 2001; Lutman *et al.*, 2013). However, we demonstrated an
252 additional benefit of delayed sowing; the difference in relative growth rate between the crop
253 and the weed is greatest at warmer temperatures, earlier in the sowing window. By delaying
254 sowing, the competitive advantage of the weed is reduced. This finding would be welcomed
255 by those seeking a boost to their weed control by delaying sowing wheat in the fields with the
256 worst weed problems.

257 The maximum reduction in *A. myosuroides* head density caused by cultivar differences was
258 reported as 52%, with a mean across multiple experiments of 30% (Lutman *et al.*, 2013). This
259 compares to the current study with a maximum difference in *A. myosuroides* biomass and,
260 therefore, seed production between the two cultivars in a given year of up to 80%. This may
261 be because there are facets of competition that the model does not capture. Below-ground
262 competition is estimated based on the proportional share of root space between the competing
263 species, which may not provide an accurate representation of acquisition of limited soil
264 resources. *In situ* validation of the model's predictions of the combined impact of cultivar
265 choice, crop density and sowing date would be of value (Deen *et al.*, 2002). It is possible that
266 there is a trade-off between early vigour (where Duxford 'wins') and later season competition
267 for below-ground resources which would have the effect of reducing the differences between
268 the cultivars. Due to the lack of data on rooting characteristics, when assessing cultivar

269 differences, the model is weighted towards above-ground early growth traits. Because of this,
270 the predictions of absolute differences need to be treated with caution. However, it is likely
271 that the pattern of the interaction with sowing rate and sowing date are more robust.

272 The model suggests that cultivar choice is a viable, low-risk alternative in weed management.
273 Cultivars are observed to differ in competitive ability in field studies (Christensen *et al.*,
274 1994; Lemerle *et al.*, 1996; Wicks *et al.*, 1986), and to work in combination with sowing
275 density (Mennan and Zandstra, 2005). Studies have reported a lack of consistency in the
276 ranking of cultivars in studies comprising of multiple years (Vandeleur and Gill, 2004). In
277 addition, the degree of weed control and tolerance to weed competition is observed to vary
278 between years. This degree of uncertainty is reflected in the model and attributed to lower
279 temperatures, perhaps compromising the ability of *A. myosuroides* to compete (Melander,
280 1995).

281 The use of a competitive cultivar has an additive affect, suggesting that similar cultivars may
282 be employed in combination with later sowing and higher crop densities to enhance weed
283 control. Many farmers are familiar with the benefits of delaying sowing and increasing
284 sowing density in order to control *A. myosuroides*, but uptake can be restricted when farmers
285 are less certain of their outcomes (Lutman *et al.*, 2013). The competitive ability of modern
286 cultivars is less understood, and its understanding is confounded by their short commercial
287 lifespan within UK agriculture (Andrew *et al.*, 2015). In order for farmers to utilise this tool,
288 they need to know the additional benefit a competitive cultivar would confer. It is proposed
289 that this is best communicated in reference to other weed control strategies. For example,
290 INTERCOM predicts that, in order for KWS Santiago to reduce yield loss to the same extent
291 as Duxford at 150 plants m⁻², it must be sown at over 600 plants m⁻². Such a high density of
292 wheat is an unrealistic target for producers due to increased risk of lodging and the cost of the
293 additional seed, making Duxford a viable alternative to increase crop competitive ability.

294 The same principle applies to sowing date. In order for KWS Santiago to match Duxford's
295 lower percentage yield loss when sown on 20 September, an approximate sowing date of 16
296 October is advised by the model. Delayed sowing has associated risks not captured by
297 INTERCOM, such as poor crop establishment or poor weather in late autumn preventing the
298 farmer from sowing the crop at all. Although maximal benefit is achieved by delaying until
299 early November, few growers are willing to risk a late sowing date (Lutman *et al.*, 2013).
300 Selecting Duxford over KWS Santiago would allow for the equivalent reduction without the
301 risk.

302 An increase to crop density and sowing date follows the principle of diminishing returns,
303 expressed as a rectangular hyperbola, which is accounted for by the model. For density, this
304 is owing to the fact that each additional wheat plant added to the stand will increase crop
305 canopy dominance by a smaller relative quantity and intraspecific competition becomes more
306 important (Cousens, 1985). As such, the use of a more competitive cultivar would produce an
307 additional benefit which cannot be acquired through increasing sowing density alone.

308 The INTERCOM model is one of the most widely-employed models of crop / weed
309 competitive interactions, and has been parameterised and validated for use in numerous
310 species combinations (Zimdahl, 2004). Here, we have used the model to demonstrate its
311 utility in predicting the behaviour of a specific crop / weed combination of immediate
312 relevance to European cereal production. However, there is the potential to take a similar
313 approach to study systems with alternative or multiple weed species (Storkey & Cussans
314 2007) to ask questions such as 'are the differences in weed suppression between cultivars
315 similar when competing with different weeds'? In these scenarios, the model could provide
316 enormous insight into the combined benefit of non-chemical control options and reduce the
317 need for large, complex experiments. It's flexibility in adjusting for growth rates, density and
318 sowing date allow it to examine crop canopy competition under different climatic conditions,

319 and it is readily adaptable to suit the crop / weed scenario of interest where light availability
320 is a crucial component in determining the outcomes of competition. A more detailed
321 understanding of below-ground competition may be required to increase the robustness of the
322 predictions when water or nutrients are limiting.

323 **5. Conclusions**

324 The INTERCOM model for wheat – *A. myosuroides* simulates IWM on final competitive
325 outcomes as would be largely expected from the literature, and implies that delayed sowing
326 date, increased crop density and competitive cultivars work well in combination. Sowing a
327 cultivar more similar to Duxford than to KWS Santiago could provide enhanced *A.*
328 *myosuroides* suppression and yield retention without the risks inherent to sowing date and
329 crop density. This approach, if applied to other crop-weed combinations, could provide
330 valuable information on IWM measures, reducing the need for repeated, expensive and long-
331 term experimentation and help growers to make better informed weed management decisions.

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336

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420 **Figure 1.** Differences between two contrasting cultivars used in the *in silico* experiments for
421 two traits: a) relative growth rate of green area ($\text{cm}^2 \text{ cm}^{-2} \text{ day}^{-1}$) calculated using the daily
422 mean temperature averaged over ten years and b) increase in plant height calculated using
423 photothermal time, (- - -) KWS Santiago, (. . .) Duxford and (—) *A. myosuroides*.

424 **Figure 2.** Interaction of crop density (100 – 400 plants m^{-2}) and sowing date (15th September
425 to 14th November) calculated as the mean output for each combination of density x date using
426 weather data from 2005-2014. In all scenarios, a weed density of 80 plants m^{-2} was used and
427 an emergence date for crop and weed of 7 and 10 days after sowing respectively.

428 **Figure 3.** INTERCOM predictions using two contrasting cultivars showing impact of
429 variable weather on a) percentage yield loss from years 2005-2014, and b) weed free wheat
430 yield; the accumulated thermal time of each year is included as the dashed line. ■ = Duxford;
431 □ = KWS Santiago. Crop density 300 plants m^{-2} , sown 20 September, *A. myosuroides*
432 density 80 plants m^{-2}

433 **Figure 4.** The seed return per plant of *A. myosuroides* (approx. 80 plants m^{-2} equiv.) when
434 grown alongside one of two cultivars (275 plants m^{-2} equiv.) across three years in a container-
435 based experiment. ■ = Duxford; □ = KWS Santiago. Mean temperature in 2011-12 was
436 8.3°C, in 2012-13 was 6.3°C and in 2013-14 was 8.9°C

437 **Figure 5.** The predicted percentage yield loss for (○) Duxford and (●) KWS Santiago when
438 sown at a) different densities (with a sowing date of 20 September) and b) different sowing
439 dates (with a crop density of 150 plants m^{-2}). In both cases, weed density was 80 plants m^{-2}
440 and dates of emergence were 10 and 7 days after sowing for the crop and weed respectively.

441

Table 1 - Parameter values for the INTERCOM model. Values for cultivar Consort are those included in the original version of the model developed for winter wheat (Storkey and Cussans, 2007). Cultivar values are those used to parameterise for respective cultivar. RWR = root weight ratio, SSA = specific stem area, SLA = specific leaf area, RGR_{GA} = relative growth rate of green area, L_0 = initial green area, a = initial height, c = height asymptote, b = maximum growth rate, m = time of the point of inflexion (just prior to achieving the asymptote).

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} ($cm^{-2} cm^{-2} tt^{-1}$)	0.0089	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

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Table 2 – The percentage yield loss predicted by INTERCOM for wheat cultivars Duxford and KWS Santiago under different crop density and sowing date combinations. \pm indicates standard error.

Cultivar	Density (plants m ⁻²)	Sowing date	
		20 September	20 October
Duxford	300	7.8 \pm 0.524	1.6 \pm 0.119
	150	11.7 \pm 0.613	2.5 \pm 0.206
KWS Santiago	300	21.7 \pm 0.953	6.6 \pm 0.441
	150	35.3 \pm 1.327	10.5 \pm 0.789

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Table 3 – The weed-free yield (t ha⁻¹) predicted by INTERCOM for wheat cultivars Duxford and KWS Santiago under different crop density and sowing date combinations. \pm indicates standard error.

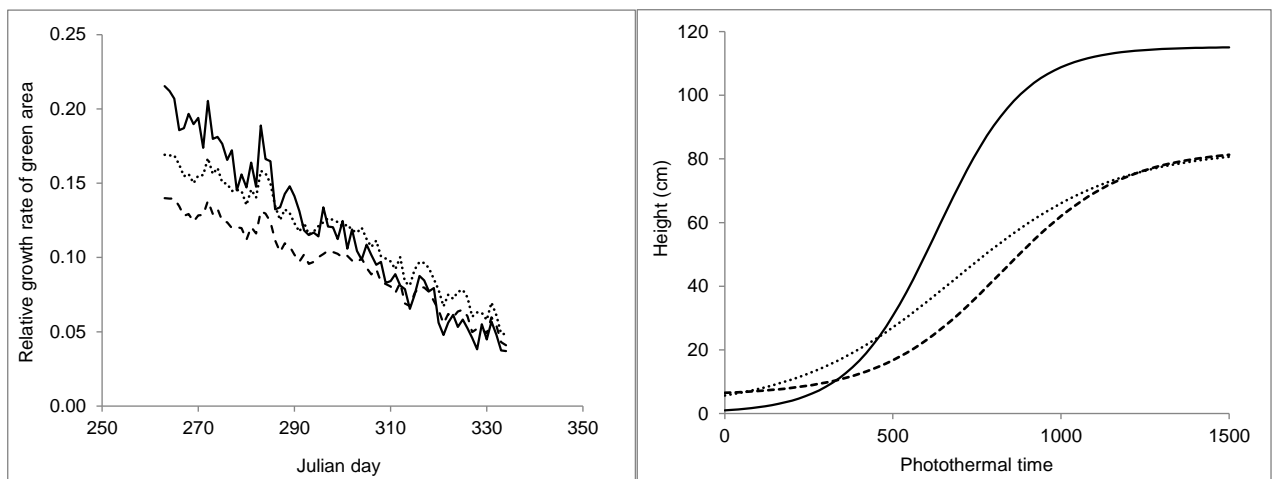
Cultivar	Density (plants m ⁻²)	Sowing date	
		20 September	20 October
Duxford	300	13.8 \pm 0.118	12.9 \pm 0.088
	150	13.7 \pm 0.122	12.9 \pm 0.087
KWS Santiago	300	13.4 \pm 0.126	12.7 \pm 0.087
	150	13.4 \pm 0.135	12.7 \pm 0.086

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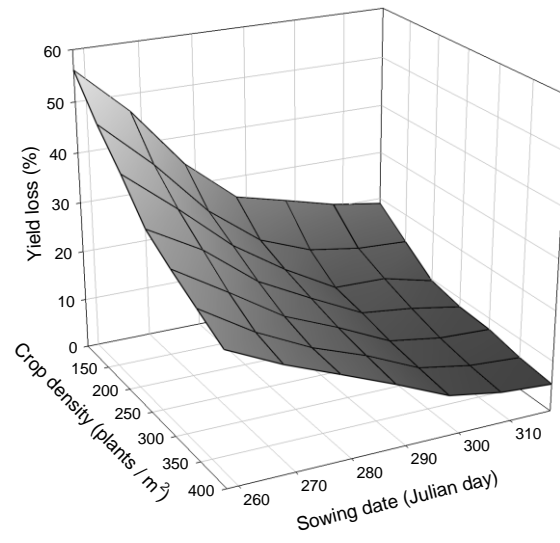
446 *Figure 1*

447 a)

b)



448 *Figure 2*



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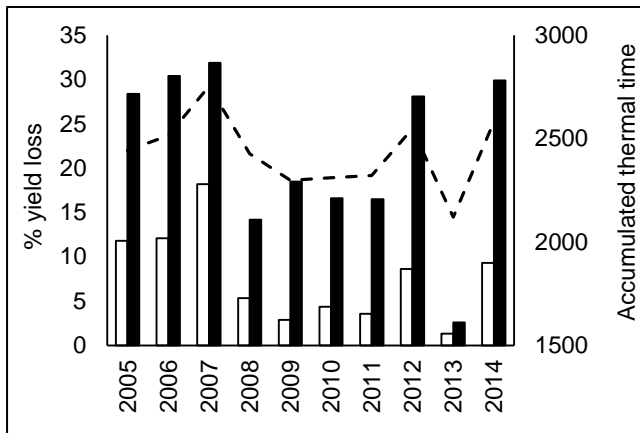
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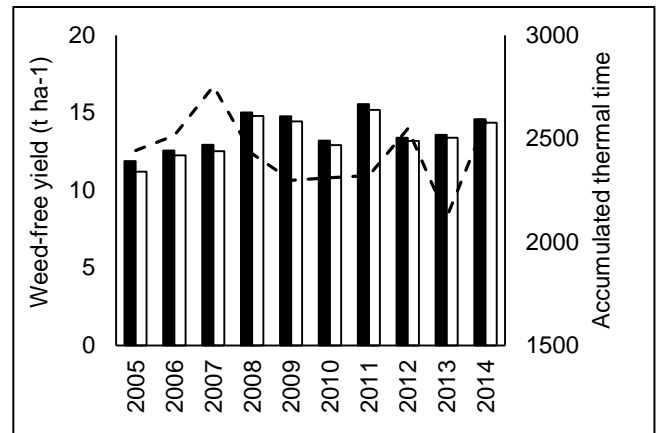
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463 Figure 3

464 a)



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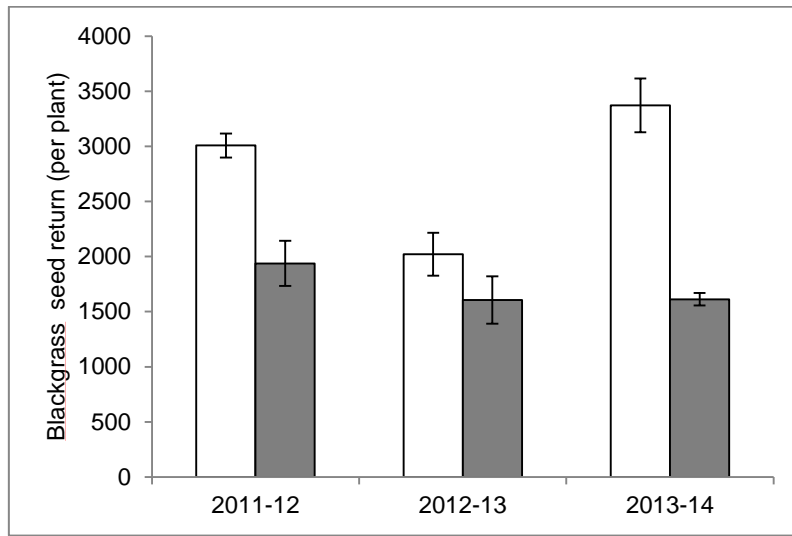
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475 *Figure 4*

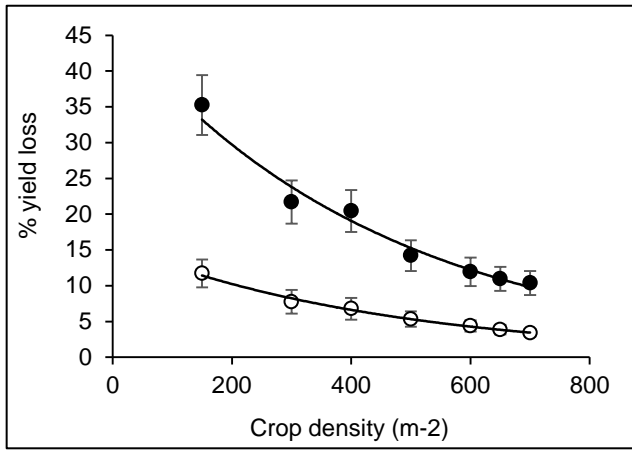


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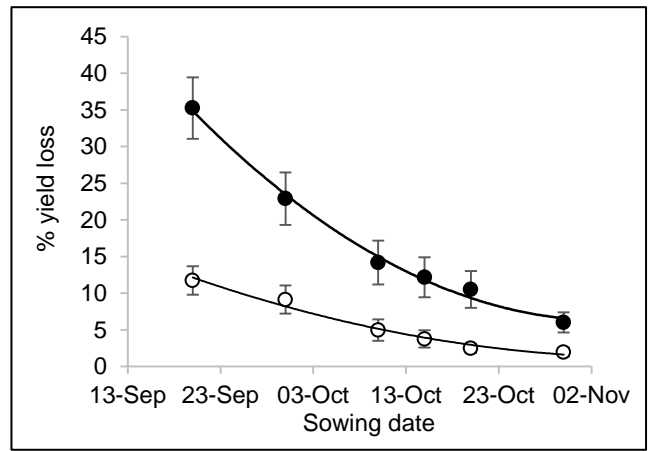
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478 Figure 5

479 a)



b)



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