

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

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2 date and cultivar choice on weed competition.

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9 Abstract:

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

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

31 **1. Introduction**

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

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 more competitive cultivars to minimise weed seed return. Within-season options, that aim to 46 47 shift the competitive balance in favour of the crop, are the focus of this paper. In most systems, non-chemical weed management options will be employed in combination with 48 49 herbicides but by increasing crop competitiveness, the required efficacy and reliance on herbicide control is reduced. In the UK, non-chemical techniques are increasingly being 50 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 (Storkey et al., 2003) and herbicide resistance is widespread in North-West Europe (Moss et 53 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 options for A. myosuroides in the UK include rotational ploughing, use of spring crops (A. 59 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).

Non-chemical control techniques are infrequently studied in combination, owing to the scale 63 of experiment required, and data are therefore lacking on whether combined effects are 64 additive, synergistic or antagonistic. Weed control measures have previously been examined 65 with the use of simulation models. Models allow a means of studying scenarios in silico, 66 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 L., the original model explained 98% of the variation in yield loss (Kropff et al., 1992) and 71 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 between crops and different weed species and is weather driven allowing variability in output 75 76 owing to environmental stochasticity to be quantified. The model can be used to examine the impact of sowing density, sowing date and crop cultivar on the outcome of crop / weed 77 78 competition.

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

84 2. Materials and methods

85 2.1. Description of the *INTERCOM* model

The INTERCOM model makes predictions of the outcomes of competition between a crop 86 and a weed based on leaf area production and distribution through the canopy in daily time 87 steps (Kropff & van Laar, 1993). The primary driving environmental variables are 88 89 photoperiod, temperature and available water. Temperature and water are growth-limiting, 90 whilst accumulated photoperiod and thermal time mediate switches between developmental stages. The model has three discrete periods. Before plants begin competing for resources, 91 growth is sink limited and modelled using an exponential relationship with biological time. In 92 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 growth of autumn and spring emerging cohorts (Storkey, 2004). A total green area index 95 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 by Spitters (1989). Precipitation data and soil water balance functions are included in the 102

model, using calculated rates of transpiration and evaporation. Water becomes limiting when
soil moisture falls below a pre-determined level, and the relationship between the potential
growth rate and water limited growth determined from an empirically derived relationship
The final phase of the model is senescence and, for wheat, grain filling. Re-allocation of
resource from stems and leaves to grain is modelled using functions from the Sirius model of
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 from the cultivar Consort (Storkey & Cussans, 2007). However, it has been frequently 115 demonstrated that wheat cultivars differ in their ability to compete against weeds. While 116 117 INTERCOM has been used in the past to inform the breeding of competitive rice cultivars (Bastiaans et al., 1997), here, we take the novel approach of using the model to quantify the 118 relative impact of cultivar choice on weed competition in the context of variable sowing rate 119 120 and sowing date. The variability in cultivar competitive ability has been attributed to numerous plant traits, including height, leaf area and developmental speed (Andrew et al., 121 2015). Many of these are traits utilised by INTERCOM to make predictions of competitive 122 123 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 frequently the poorest performer (Andrew, 2016). Using data collected from a series of 129 130 outdoor, container-based experiments based at Rothamsted Research, UK, data were available to parameterise the model for different cultivars. To parameterise seedling growth 131 132 rate, the protocol used in Storkey (2004) was followed; sequentially sampling seedlings over a two month period. For parameters determining resource competition, the cultivars were 133 grown in competition with A. myosuroides in outdoor containers (40 x 32 cm) in a fully 134 135 replicated experimental design repeated over three years and a range of morphological traits measured through the season. A selection of the original model parameters for wheat (cv. 136 137 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

A number of *in silico* experiments were done using INTERCOM. Firstly, data input for INTERCOM can be amended to reflect the density of wheat and *A. myosuroides* in the stand and wheat sowing date; the interaction of these two factors was analysed using the original parameters for the cultivar, Consort. Crop densities between 100 and 400 wheat plants m⁻² were selected to represent the potential to increase the competitive ability of the wheat 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 November). Emergence times after sowing were kept constant at seven days for A. 152 myosuroides and 10 days for wheat, and the A. myosuroides density was maintained at 80 153 plants m⁻² across all simulations. To quantify the interaction of sowing date and sowing rate 154 155 on crop canopy competitiveness, the model was run using 49 combinations of rate x date, using intervals of 50 plants m^{-2} for crop density and 10 days for sowing date. The simulation 156 model was run using radiation, temperature and precipitation data recorded at Rothamsted 157 meteorological station for harvest years 2005-2014, providing yearly predictions of 158 percentage crop yield loss and A. myosuroides above-ground dry weight (m⁻²). 159

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

environmental variability using ANOVA. All statistical analysis of data was conducted inGenstat 16 (VSN International, 2013).

177 **3. Results**

In the model's predictions, percentage yield loss and A. myosuroides biomass at maturity 178 179 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 be positively correlated, allowing the output to be used to predict seed return under different 182 scenarios. An increase of 10% yield loss was associated with approximately 15000 additional 183 184 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 both cases the relationship was non-linear (Figure 2). 186

187

Figure 2 near here

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

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Figure 3 & 4 near here

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Accumulated thermal time was an important determinant of yield loss predictions in the INTERCOM model for both cultivars, with lower temperatures resulting in decreased yield 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 was in the warmest year (2006), with 17% yield loss. The predicted weed-free yield of wheat suffered no equivalent detriment in the colder years (Figure 3b), implying that temperature has a stronger impact on *A. myosuroides* competitive performance.

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Figure 5 near here

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

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

The effects of changing crop cultivar, sowing density and sowing date on weed-free yield was restricted only to sowing date, with delayed sowing resulting in a mean decrease in yield 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*

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

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

228

Figure 5 near here

229 4. Discussion

There are various non-chemical control strategies available to farmers, and these are often 230 231 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 complicated to analyse. The use of simulation models such as INTERCOM can provide 235 valuable insight into their combined effect on crop-weed competitive interactions (van 236 237 Ittersum et al., 2003).

The predictions of the reduction in yield loss with increasing crop density were in agreement with the published literature (Mennan and Zandstra, 2005). The model predicted an average reduction in seed production of 25% when crop density was increased from 100 to 300 plant m⁻². This is an equivalent increase in crop competitiveness as was reported in Lutman *et al.* (2013) where these treatments resulted in reductions in *A. myosuroides* head density of 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. myosuroides scenario, the crop acquires a competitive advantage when sown at higher 248 249 densities and at later sowing dates. The benefit of increased sowing density has been observed in various crop-weed associations (Christensen et al., 1994; Melander, 1995; Cosser 250 251 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 worst weed problems. 256

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

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

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

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 control. Many farmers are familiar with the benefits of delaying sowing and increasing 283 284 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 cultivars is less understood, and its understanding is confounded by their short commercial 286 287 lifespan within UK agriculture (Andrew et al., 2015). In order for farmers to utilise this tool, they need to know the additional benefit a competitive cultivar would confer. It is proposed 288 289 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 as Duxford at 150 plants m⁻², it must be sown at over 600 plants m⁻². Such a high density of 291 wheat is an unrealistic target for producers due to increased risk of lodging and the cost of the 292 293 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 farmer from sowing the crop at all. Although maximal benefit is achieved by delaying until 298 299 early November, few growers are willing to risk a late sowing date (Lutman et al., 2013). Selecting Duxford over KWS Santiago would allow for the equivalent reduction without the 300 301 risk.

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

The INTERCOM model is one of the most widely-employed models of crop / weed 308 309 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 utility in predicting the behaviour of a specific crop / weed combination of immediate 311 312 relevance to European cereal production. However, there is the potential to take a similar approach to study systems with alternative or multiple weed species (Storkey & Cussans 313 314 2007) to ask questions such as 'are the differences in weed suppression between cultivars similar when competing with different weeds'? In these scenarios, the model could provide 315 316 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,

and it is readily adaptable to suit the crop / weed scenario of interest where light availability
is a crucial component in determining the outcomes of competition. A more detailed
understanding of below-ground competition may be required to increase the robustness of the
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 cultivar more similar to Duxford than to KWS Santiago could provide enhanced A. 327 328 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 valuable information on IWM measures, reducing the need for repeated, expensive and long-330 331 term experimentation and help growers to make better informed weed management decisions.

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337 **References**

Andrew, I.K.S., Storkey, J.S., Sparkes, D. 2015. A review of the potential for competitive
cereal cultivars as a tool in integrated weed management. Weed Res. 55, 239-248.

Andrew, I.K.S. 2016. Identifying and evaluating competitive traits in wheat for sustainable
weed management. Ph.D. Thesis. University of Nottingham.

- 342 Barzman, M., Barberi, P., Birch, A.N.E., Boonekamp, P., Dachbrodt-Saaydeh, S., Graf, B.,
- Hommel, B., Jensen, J.E., Kiss, J., Kudsk, P., Lamichhane, J.R., Messean, A., Moonen, A.C.,
- Ratnadass, A., Ricci, P., Sarah, J.L., Sattin, M., 2015. Eight principles of integrated pest
 management. Agron. Sustain. Dev. 35, 1199-1215.
- Bastiaans, L., Kropff, M.J., Kempuchetty, N., Rajan, A., Migo, T.R. 1997. Can simulation
- 347 models help design rice cultivars that are more competitive against weeds? Field Crops Res.348 51, 101-111.
- Bastiaans, L., Paolini, R., Baumann, D.T. 2008. Focus on ecological weed management: whatis hindering adoption? Weed Res. 48, 481-491.
- Bond, W., Grundy, A.C. 2001. Non-chemical weed management in organic farming systems.
 Weed Res. 41, 383-405
- Christensen, S., Rasmussen, G. Olesen, J.E. (1994) Differential weed suppression and weed
 control in winter wheat. Asp Appl Biol. 40, 335-342.
- Cosser, N.D., Gooding, M.J., Thompson, A.J., Froud-Williams, R.J. 1997. Competitive
 ability and tolerance of organically grown wheat cultivars to natural weed infestations. Ann
 Appl Biol. 130, 523-535.
- Cousens, R. 1985. A simple model relating yield loss to weed density. Ann Appl Bio. 107,239-252.
- 360 Deen, W., Cousens, R., Warringa, J., Bastiaans, L., Carberry, P., Rebel, K., Riha, S., Murphy,
- 361 C., Benjamin, L.R., Cloughley, C., Cussans, J., Forcella, F., Hunt, T., Jamieson, P.,
- 362 Lindquist, J., Wang, E. 2003. An evaluation of four crop : weed competition modeuls using a
- 363 common data set. Weed Res. 43, 116-129.

- Heap, I.M. 1997. The occurrence of herbicide-resistant weeds worldwide. Pestic Sci. 51, 235243.
- Jamieson, P.D., Semenov, M.A., Brooking, I.R., Francis, G.S., 1998. Sirius: a mechanistic
 model of wheat response to environmental variation. Eur. J. Agron. 8, 161-179.
- Keshtkar, E., Mathiassen, S.K., Moss, S.R., Kudsk, P. 2015 Resistance profile of herbicideresistant *Alopecurus myosuroides* (black-grass) populations in Denmark. Crop Prot. 69, 8389.
- 371 Kropff, M.J., Spitters, C.J.T. (1992) An ecophysiological model for interspecific competition,
- applied to the influence of *Chenopodium-album* L on sugar-beet. 1. Model description and
- arameterization. Weed Res. 32, 437-450.
- Kropff, M.J., Spitters, C.J.T., Schnieders B.J., Joenje, W. and De Groot W. (1992) An
 ecophysiological model for interspecific competition, applied to the influence of *Chenopodium-album* L on sugar-beet. 2. Model evaluation. Weed Res. 32, 451-463.
- 377 Kropff, M.J., van Laar, H.H. 1993. *Modelling crop-weed interactions*. Wallingford, UK:
 378 CAB International.
- Lemerle, D., Verbeek, B., Cousens, R.D., Coombes, N.E. 1996. The potential for selecting
 wheat varieties strongly competitive against weeds. Weed Res. 36, 505-513.
- 381 Lutman, P.J.W., Moss, R., Cook, S., Welham, S.J. 2013. A review of the effects of crop
- agronomy on the management of *Alopecurus myosuroides*. Weed Res. 53, 299-313.
- 383 Melander, B. 1995. Impact of drilling date on *Asper spica-venti* and *Alopecurus myosuroides*
- in winter cereals. Weed Res. 35, 157-166.

- Mennan, H., Zandstra, B.H. 2005. Effect of wheat (*Triticum aestivum*) cultivars and seeding
 rate on yield loss from *Galium aparine* (cleavers). Crop Prot. 24, 1061-1067.
- 387 Moss, S.R., Marshall, R., Hull, R., Alarcon-Reverte R. 2011. Current status of herbicide-
- resistant weeds in the United Kingdom. Asp App Biol. 106, 1-10.
- 389 Oerke, E.-C. 2006. Crop losses to pests. J Agr Sci. 144, 31-43.
- Roberts, J.R., Peeper, T.F., Solie, J.B. 2001. Wheat (*Tricium aestivum*) row spacing, seeding
- rate, and cultivar affect interference from rye (*Secale cereal*). Weed Technol. 15, 19-25.
- 392 Spitters, C.J.T (1989) Weeds: population dynamics, germination and competition. In:
- 393 Simulation and Systems Management in Crop Protection. (eds. R Rabbinge, SA Ward and
- HH van Laar), pp182-216. Simulation Monographs, Pudoc, Wageningen.
- Storkey, J., 2004. Modelling seedling growth rates of 18 temperate arable weed species as afunction of the environment and plant traits. Annals of Botany 93, 681-689.
- Storkey, J., Cussans, J.W., Lutman, P.J.W, Blair, A.M. (2003) The combination of a
 simulation and an empirical model of crop/weed competition to estimate yield loss from *Alopecurus myosuroides* in winter wheat. Field Crop Res. 84, 291-301.
- Storkey, J., Cussans, J.W. 2007. Reconciling the conservation of in-field biodiversity with
 crop production using a simulation model of weed growth and competition. Agr Ecosyst
 Environ. 122, 1421-1429.
- Storkey, J., Holst, N., Bojer, O.Q., Bigongiali, F., Bocci, G., Colbach, N., Dorner, Z.,
 Riemens, M.M., Sartorato, I., Sonderskov, M., Verschwele, A., 2015. Combining a weed
 traits database with a population dynamics model predicts shifts in weed communities. Weed
 Research 55, 206-218.

- 407 Vandeleur, R.K., Gill, G.S. 2004. The impact of plant breeding on the grain yield and408 competitive ability of wheat in Australia. Aust J Agr Res. 55, 855-861.
- 409 van Ittersum, M.K., Leffelaar, P.A., van Keulen, H., Kropff, M.J., Bastiaans, L., Goudriaan,
- J., 2003. On approaches and applications of the Wageningen crop models. Eur. J. Agron. 18,
 201-234.
- 412 VSN International. 2013. Genstat for Windows 16th Edition. VSN International, Hemel
 413 Hempstead, UK.
- Weaver, S.E. 1996. Simulation of crop-weed competition : Models and their applications.
 Phytoprotection. 77, 3-11.
- Wicks, G.A., Nordquist, P.T., Baenziger, P.S., Klein, R.N., Hammons, R.H., Watkins, J.E.
 2004. Winter wheat cultivar characteristics affect annual weed suppression. Weed Technol.
 18, 988-998.
- 419 Zimdahl, R.L. 2004. *Weed-crop competition: a review*. 2nd Edn. Blackwell, Oxford.

Figure 1. Differences between two contrasting cultivars used in the *in silico* experiments for two traits: a) relative growth rate of green area (cm² cm⁻² day⁻¹) calculated using the daily mean temperature averaged over ten years and b) increase in plant height calculated using photothermal time, (- - -) KWS Santiago, (. . .) Duxford and (—) *A.myosuroides*.

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

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

Figure 4. The seed return per plant of *A. myosuroides* (approx. 80 plants m⁻² equiv.) when grown alongside one of two cultivars (275 plants m⁻² equiv.) across three years in a containerbased experiment. \blacksquare = Duxford; \square = KWS Santiago. Mean temperature in 2011-12 was 8.3°C, in 2012-13 was 6.3°C and in 2013-14 was 8.9°C

Figure 5. The predicted percentage yield loss for (\bigcirc) Duxford and (\bullet) KWS Santiago when sown at a) different densities (with a sowing date of 20 September) and b) different sowing dates (with a crop density of 150 plants m⁻²). In both cases, weed density was 80 plants m⁻² and dates of emergence were 10 and 7 days after sowing for the crop and weed respectively.

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).

	Consort		
	(Storkey &		
	Cussans,		KWS
Trait	2007)	Duxford	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
Logistic functions for			
height			
<i>a</i> (cm)	7.4	1.36	5.73
<i>c</i> (cm)	77.9	81.845	77.299
$b (\text{cm ptt}^{-1})$	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.

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

		20 September	20 October	
Cultivar	Density	Souving data		
	(plants m^{-2})	Sowing date		
Duxford	300	13.8 ± 0.118	12.9 ± 0.088	
	150	13.7 ± 0.122	12.9 ± 0.087	
KWS	300	13.4 ± 0.126	$12.7 \pm 0.087 $	
Santiago	150	13.4 ± 0.135	12.7 ± 0.086	

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446 Figure 1

a)





b)

Figure 2



Figure 3



b)









