The costs of human-induced evolution in an agricultural system

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Abstract

Pesticides have underpinned significant improvements in global food security, albeit with associated environmental costs. Currently, the yield benefits of pesticides are threatened as overuse has led to wide-scale evolution of resistance. Yet despite this threat, there are no large-scale estimates of crop yield losses or economic costs due to resistance. Here, we combine national-scale density and resistance data for the weed *Alopecurus myosuroides* (black-grass) with crop yield maps and a new economic model to estimate that the annual cost of resistance in England is £0.4bn in lost gross profit (2014 prices), and annual wheat yield loss due to resistance is 0.8 million tonnes. A total loss of herbicide control against black-grass would cost £1bn and 3.4 million tonnes of lost wheat yield annually. Worldwide, there are 253 herbicide-resistant weeds, so the global impact of resistance could be enormous. Our research provides an urgent case for national-scale planning to combat further evolution of resistance, and an incentive for policies focused on increasing yields through more sustainable food-production systems rather than relying so heavily on herbicides.

Resistance to xenobiotics (e.g. antibiotics, antimycotics, pesticides), caused by high frequency of application[1–4], is a severe and growing economic[5], food security[1,6] and public health crisis[3,6,7]. In the past, pesticides have enabled increases in food production but growing loss of their efficacy is now reducing yields[1,8]. This is a threat to global food security. Despite this, there are currently no large-scale estimates of the effects of pesticide resistance on crop yields.

Future food security will rely on sustainable intensification[9,10], which aims to boost yields from the same area of land but with reduced environmental impact. Pesticide resistance threatens both these goals: yields are threatened by higher pest densities[1,8], and the environment is threatened because the usual response to resistance has been increased pesticide use[11,12] – despite the knowledge that pesticides harm water and soil quality and biodiversity[12–15]. In an era of increasing population and extreme competition for land, there is strong motive to investigate any phenomenon that jeopardises food security. Furthermore, as pesticide resistance is implicated in three elements of the UN's water-food-energy-ecosystems nexus, there is an obvious incentive to assess its impacts.

National- and global-scale economic costs of xenobiotic resistance are poorly quantified but, where this has been attempted in human healthcare settings for anti-microbial resistance, costs run into billions[16] or trillions[17] of dollars and even these enormous numbers are thought to be underestimates[5]. In agriculture, large-scale cost estimates are lacking but anecdotal evidence[18] combined with crop areas suggests that, in the US, increased chemical costs due to glyphosate resistance may exceed $10bn annually. Costs due to yield loss would further increase this figure.

The likely magnitude of the social, economic and environmental costs means a co-ordinated global policy response, driving governance integration across sectors, is urgently needed[19]. In healthcare, the World Health Organisation endorsed a Global Action Plan for anti-microbial resistance in 2015; however, there is no equivalent in animal and crop production. This is despite the fact that agriculture accounts for 37% of land use globally (World Bank Open Data, 2018), an estimated 4 million tonnes of pesticides are applied worldwide each year (FAOStat, 2019), resistance to pesticides is well documented[20–23], and there is a long-term upward trend in pesticide use[24]. United Nations resistance advice (Guidelines on Prevention and Management of Pesticide Resistance, FAO 2012) and a handful of informal, largely agrochemical industry-led, groups exist (e.g. CropLife International, IRAC, AHDB resistance action groups), but the lack of government involvement means that problems of resistance continue. Furthermore, even in healthcare where a global plan exists, creation of national action plans is hampered by a lack of evidence, particularly on the true costs of resistance and the cost-effectiveness of policies[25]. Determining the national costs associated with xenobiotic resistance is a critical first step in creating a national action plan.

We address this issue for herbicide resistance in the UK. Mirroring the global state of affairs, the UK has a national Antimicrobial Resistance Strategy but no national resistance policy in place for other classes of xenobiotic such as pesticides. This is despite (a) a continuing upward trend in the area to which pesticide is applied (FERA PUS stats, 2019), (b) evidence that resistance is impacting output[1] and (c) UK government awareness of the issue (POSTnote 501, 2015). Here, we combine a national-scale dataset of the density and resistance status of the most economically significant weed in western Europe[26], black-grass (*Alopecurus myosuroides*), with 10 years' worth of past management history, corresponding yield data (Figure 1) and a new economic model (Supplementary Methods) to estimate the economic and food production impacts of herbicide-resistant black-grass in England. Using this approach, we provide the first national-scale estimate of yield losses and the full economic costs due to herbicide resistance. We distinguish between losses due to weed infestation, I (i.e. both resistant and susceptible plants) and losses due to resistant plants, R. The magnitude of our results suggests a pressing need for governmental action to address resistance issues, and for other countries to undertake their own national-scale assessments.

Costing resistance at the field scale

Estimated yield loss due to black-grass infestation in winter wheat was, on average, 0.4 t ha^{-1} (Table 1), or 5% of the average estimated potential wheat yield (8.3 t ha^{-1}) in the absence of black-grass. We estimated this by applying yield penalties due to black-grass infestation (Figure 1) to the crop yield estimation component in our economic model (details in Methods and SI). Resistance frequencies were then used (c.f. Methods) to calculate that most of this lost yield (0.38 t ha^{-1}) was due to resistant plants. At low densities of black-grass the yield loss was negligible, whereas at the highest weed densities mean yield loss was 1.8 t ha^{-1}, 100% of which was due to resistant plants (Table 1 and Figure 3).

The mean economic cost of resistance (C_R, defined as the production losses and additional costs due to resistant black-grass) in winter wheat was £75 ha^{-1} at low black-grass density and £450 ha^{-1} at very high density (Table 1 & Figure 2c). Estimates of C_R will vary, potentially greatly, according to the input and output prices used, but the costs calculated here using 2014 prices represent 7% and 37%, respectively, of potential gross profit from winter wheat in these fields in the absence of resistant black-grass, and compare to average total agricultural costs (English cereal farms, 2014) of £1,076 ha^{-1} (Farm Business Survey Region Reports, 2019). Across all density states, the mean C_R in winter wheat was £155 ha^{-1} (Table 1), or 14% of potential gross profit. C_R within density states varied widely, ranging from £0-493 ha^{-1} in winter wheat fields with low black-grass density, to £355-773 ha^{-1} in fields with very high densities (raw data not shown). At very high density states, 100% of the total costs of black-grass infestation came from resistant plants (Table 1 and Figure 3).

Across a rotation, the mean C_R in low density fields was £58 ha^{-1}, and £280 ha^{-1} in very high density fields (Table 1). Again, 100% of the costs were due to resistant plants in fields with very high black-grass density, whereas in low density fields just under 70% of costs came from resistant plants. The per-hectare C_R in winter wheat was higher than the per hectare C_R across a rotation (Table 1 and Figure 2c & d) due to the negative impact of the weed on wheat yield (no yield penalties were applied to other crops in the rotation). Overall, as average black-grass density increases, so does the proportion of the cost or yield loss that is due to resistant plants (Table 1), in line with previous findings[1] that resistance drives weed abundance. Field-scale resistance impacts are thus greater in regions with higher black-grass densities, especially in winter wheat crops (Figure 2), and resistance impacts in the UK reduce along a gradient from south to north (see Figure 4). See Methods for a discussion of the assumptions that underpin these estimations.

The use of herbicides targeting black-grass in winter wheat did not differ across different final (pre-harvest) densities of weed infestation (χ^2_1=0.0982, p=0.754, Figure 3b and Supplementary Figure 5). Thus, in fields with low final black-grass density, herbicide costs constituted 82% of total costs (this applies to both the cost of infestation, C_I, and to C_R), whereas in fields with high and very high final black-grass densities, the biggest source of lost income was yield loss (60% and 77% respectively, Figure 3). In some of the low density fields, relatively intense herbicide use will be justified where high levels of susceptibility remain in the weed population and, therefore, where these herbicides are still effective in reducing yield loss potential. However, in low density fields with high levels of herbicide resistance (in our data, 75% of fields with low and medium black-grass density had high resistance (>60% survival) to Atlantis), intense herbicide application may be counter-productive as (a) herbicide costs will outweigh benefits of black-grass control, (b) it will impose an unnecessary environmental burden[12,27–29] and (c) it will have the unwanted effect of selecting for even higher frequencies of resistance within populations[1,30]. In these situations, a reduction in herbicide use may bring economic benefits but would need to be accompanied by cultural and physical control methods to maintain low weed population sizes as part of an integrated weed management programme. We expand on this in the discussion.

The impact of resistance at a national scale

Total annual wheat yield loss for England was 0.86 million tonnes (mt; Supplementary Table 5), almost all of which (0.82 mt) was due to resistant plants (Figure 4a and Supplementary Table 6). Sensitivity analyses suggest that annual wheat yield losses due to resistant black-grass (YL_R) in England may be as low as 0.3 mt or as high as 3 mt (Supplementary Table 11) given uncertainties in our yield penalty estimates (further details in SI). Whichever figure we accept, our estimates run counter to global goals of increased yields[31–33] and are particularly concerning in view of the current wheat yield stagnation in NW Europe[34,35]. UK annual domestic wheat consumption hovers around 15 million tonnes (DEFRA); the highest yield loss values from our sensitivity analyses represent nearly a fifth of this.

In terms of economics, the total annual cost of black-grass infestation in England was £0.44bn across all crops (termed *rotation cost* from now on, Supplementary Table 5), £0.38bn p.a. of which was due to resistant plants (Figure 4b, Supplementary Table 6). In winter wheat crops, C_I was £0.35bn p.a., of which C_R was £0.31bn (Figure 4c, Supplementary Table 6). At a regional scale, some rotation costs are higher than those in winter wheat. This is because, although field-scale rotation costs are lower than those in winter wheat, the total cereal crop area is much larger than the winter wheat area and so the scaled-up rotation costs are relatively higher. In the West Midlands (WM) and South East (SE) the average C_R per ha in winter wheat crops was particularly high compared to other regions (WM £387 ha^{-1}, SE £270 ha^{-1}, EM £159 ha^{-1}, EE £206 ha^{-1}, YH £88 ha^{-1}, abbreviations as in Figure 4); as a result, the scaled-up costs in these two regions remained higher in winter wheat than across rotations. Values for the SE region should be treated with caution as we used just eight fields from this region in our analysis and all of them were concentrated in one area (where there are high densities of resistant black-grass[1], see Supplementary Figure 3). The estimates for this region are therefore unlikely to be very representative of the entire region.

Sensitivity analyses showed that annual rotation C_R might be as low as £0.3bn p.a. or as high as £0.8bn p.a. (Supplementary Table 11). Nevertheless, even at the lower end, the costs are very large. To put these figures into perspective, total income from all types of farming in England was £3.9bn in 2014. Herbicide resistance is therefore having a severe impact on English arable farming, and these results underscore the need to manage resistance through coordinated action at a national level.

Potential costs and crop losses

Because resistance is increasing over time and driving black-grass density[1], we also estimated yield losses and costs in winter wheat under a total loss of herbicide control (Figure 2b & e) by assuming that all quadrats in every field were in a very high density state and that 100% of costs and yield losses were due to resistant plants (cf. Methods). Under this scenario of ubiquitous very high black-grass density, wheat YL_R ranged from 1.4 – 2.3 t ha^{-1} and on average was 2 t ha^{-1}, representing over a quarter (28%) of average potential estimated wheat yield (8.3 t ha^{-1}) in the absence of black-grass. The C_R in winter wheat under this scenario ranged from £294 ha^{-1} to £904 ha^{-1}, and on average was £467 ha^{-1}. This means that, if the problem continues unchecked, the costs of infestation in winter wheat could approach half of the average agricultural costs on English cereal farms (£1,076 ha^{-1}). We do not suggest that such a scenario will occur; however, it is worth estimating these impacts (a) to illustrate the potential consequences of inaction and loss of glyphosate and/or pre-emergence black-grass herbicides, and (b) to present a frame of reference, allowing the extent of the current situation to be assessed in relation to the worst possible case.

Scaling up these 'worst-case' estimates we find that potential YL_R in English winter wheat under a scenario of total loss of herbicide control is 3.4 mt yr^{-1} (95% CI 3.3 – 3.6 mt, Supplementary Table 7), representing just under a quarter of UK domestic wheat consumption. Potential annual rotation C_R is £1bn (95% CI £0.9bn – £1.0bn, Supplementary Table 7). To present a more conservative worst-case estimate, we also estimated YL_R and C_R using just those fields in the top quintile and top decile of the black-grass density range: these gave potential annual yield losses in winter wheat of 2.1 mt and 2.6 mt respectively, and rotation C_R of £0.8bn (Supplementary Table 8).

A comparison of current and potential yield loss (Supplementary Tables 6 *versus* 7) shows that yield loss in the worst case scenario could be four to six times greater than it is now, except towards the northern edge of the black-grass range where it is seventeen times higher, reflecting the fact that herbicide resistant black-grass is not yet such a pressing problem in this area. The only region in which current resistance impacts are closer to potential impacts is in the South East, where a large proportion of fields have very high average black-grass density (Supplementary Figure 3); however, as previously mentioned, estimates for the South East are unlikely to be very representative of the region and should be viewed with caution.

C_R under the worst case scenario is around two-and-a-half to three times the current C_R, except in winter wheat in northern regions: here, potential C_R in winter wheat is around nine times current C_R, again reflecting the fact that resistance is not yet so widespread in northern areas of England. To contextualise these costs in terms of the agrochemicals market, in 2014 herbicides contributed £0.2bn to the UK National Agrochemical Market, the total value of which was £0.6bn (ECPA Industry Statistics, 2018). Some of our estimates of the costs of resistance in England are greater than the entire value of herbicides to the UK agrochemicals market.

Our estimates indicate that low black-grass densities currently account for just over half of England's wheat producing area (Supplementary Figure 3) so there is a strong incentive to prevent densities increasing. In Europe, resistant black-grass has been recorded in 14 countries, including Europe's top wheat producers (Germany and France; Eurostat, 2018). European wheat consumption is forecast to increase slightly over the next 10 years, so we urge wheat-producing countries to undertake their own national-scale resistance impact assessments.

Discussion

Here we report the first national-scale estimate of the impacts of human-induced evolution of herbicide resistance. The scale of our findings illustrates that pesticide resistance has implications for national food security and economics. Annual potential losses of the order of 3 mt and £1bn are large enough that national-scale policy measures are needed to reduce the impact and spread of resistance.

Resistance management is currently the responsibility of individual practitioners, whose collective actions constitute a national response. However, when pesticides are effective, there is an economic incentive for individual practitioners to use them and to crop mostly high value crops such as winter wheat. This behaviour is unsustainable as it drives resistance[1,30], which we show has a negative impact on crop yields and income nationally. Our results thus imply that leaving resistance management to individual practitioners is an inadequate approach and that a national, targeted response is required. There is precedent for regulating pesticide use through policy in environmental and health arenas: there is now an urgent need for national-scale policy to regulate pesticide use in relation to resistance impacts on yield and economics.

When designing resistance management policy, governments should adopt a nexus approach and explicitly link the economic, agricultural, environmental and health aspects of this issue. Joined-up legislation could help encourage this: in Europe, for example, resistance management could be incorporated into existing legislation such as the EU Directive on the Sustainable Use of Pesticides (Directive 2009/128/EC), which already legislates to reduce pesticide risk to human health and the environment. Integration of these different policy arenas could help ensure that legislation for reduced pesticide use based on environmental or health concerns also delivers resistance management benefits, and *vice versa* : from environmental and sustainability policy perspectives, the impacts estimated here could be used as a lever to further justify, in both food security and economic terms, reduced pesticide use through practices like integrated pest management (IPM).

Resistance management policy could be implemented via a national action plan, which should aim to (a) reduce the spread of resistance into unaffected areas, and (b) find, and communicate, non-chemical ways of reducing high weed populations in regions that already have high resistance. A key aspect of such an action plan will be to reduce use of, and reliance on, pesticides, because use is driving resistance. Reduced use has already been recommended for other classes of xenobiotic, such as in the management of insect vectors of human disease[36], and has been implemented for prostate cancer[37]. This reduction in pesticide use could be achieved by improving crop rotation and employing other IPM practices such as seedbed sanitation, careful choice of sowing dates and densities, direct sowing, physical control methods, field hygiene measures and regular monitoring[38–40].

Because resistance management is likely to be a contentious issue, we suggest that a national action plan should be formulated after public consultation and a process of consensus-building and collaboration[41]. Providing the public with high-quality evidence and information is crucial to the success of these consultations: an assessment of the economic outcomes of reducing herbicide use, and of the cost-effectiveness of a range of potential policies or mitigation strategies, would thus be a useful next step, both for the consultation process and for subsequent policy design.

It is likely that statutory limits on pesticide use will be necessary, and that incentives and enforcement will be required to achieve behaviour change. Agricultural policy could be used to incentivise and support farmers to change their management practices, for example by stipulating improved crop rotation to qualify for income support or by providing support payments during the initial phase of reducing pesticide use and increasing IPM. This would be especially important in those areas where resistance is not currently a problem, and it would therefore be useful to estimate the short-term opportunity cost to individual practitioners of reducing pesticide use in areas with low resistance. Alternatively, governments could incorporate resistance management into Payments for Ecosystem Services schemes (or set up such schemes where none exist) whereby farmers are rewarded for outcomes such as improved water quality or biodiversity, or maintenance of pesticide susceptibility in pest populations. Governments could also leverage commercial interest, for example by introducing tax incentives for water companies to set up farmer advisory or support schemes to help reduce pesticide use. Enforcement could take the form of caps on pesticide use and fines for breaking those limits or for spreading resistant weed seeds. Additionally, governments could legislate for disincentives to the herbicide manufacturing industry – for example by higher taxation rates on sales over a threshold volume – and could help reduce the influence of the agrochemicals industry by allocating public money to fund farm advisory services as well as research and development.

Finally, any pesticide resistance policy must also target glyphosate resistance. Glyphosate resistant weeds are already found on almost every continent[20] but are not yet present in the UK. However, English farmers are increasingly reliant on glyphosate to control herbicide-resistant black-grass and as a result there has been a dramatic increase in its use[42], ramping up the evolutionary pressure on black-grass to develop resistance to glyphosate, too[30]. In the US, widespread glyphosate resistance is already a reality and the scale of the problem dwarfs that being faced with black-grass in England. A US-wide assessment of resistance-related costs and yield losses should be undertaken as a matter of urgency to inform national food-security planning. Worldwide there are many pesticide-resistant species[23,43,44]. Our findings should therefore be a catalyst to other countries to develop national-scale estimates of the impacts of resistance as a first step in assessing the need for their own pesticide resistance strategies.

Methods

Field data. Field management data was obtained for years 2004 – 2014. Black-grass (BG) density and resistance, and winter wheat yield, was sampled from 2014-2017. For details see reference 1. BG density states are given in Supplementary Table 10. To estimate costs of resistance, we used a subset of 66 fields from the full dataset (138 fields), and field management histories up to 2014. This subset comprised fields with ≥3 years' management history and with complete historical data on tillage operations and herbicide applications. Where soil type was not specified by the farmer, we extracted soil type from the National Soil Resources Institute NATMAP1000 database (Soils Data © Cranfield University (NSRI) and for the Controller of HMSO [2016]). We used BG density data from all 138 fields in the scaling-up process.

The cost of BG infestation (C_I) comes mainly from two factors: (i) the direct impact of BG on wheat yield through competition; (ii) the cost of herbicides targeting BG (which may also be applied in crops other than wheat) and their application. There are also some additional, lesser costs, for example those incurred for an inversion plough. With respect to herbicides, we were interested only in calculating costs related directly to BG infestation: in the field management dataset, we therefore identified all herbicide applications specifically targeting BG. For all other herbicide costs (i.e. adjuvants, desiccants, and applications not specifically targeting BG) we calculated an average value per crop from our dataset and incorporated this into the sundry costs in BGRI-ECOMOD. For the thirteen observations where farmers had grown crops not included in BGRI-ECOMOD, we used proxy crops. Spring oilseed rape was the proxy for borage, millet and mustard (1 observation of each); ware potatoes were the proxy for onions (1 observation); and barley was the proxy for oats (7 observations) and triticale (2 observations).

Economic model. We custom-built an economic model, BGRI-ECOMOD, capable of incorporating a wide range of farm management options and including a user-specified yield penalty for varying levels of weed infestation. The model code supplied incorporates the mean yield penalties from our data (see Figure 1 and SI); however, we enable users to specify yield penalties so that BGRI-ECOMOD can be used for different weed species, or be updated in light of new BG yield penalty data, or for running sensitivity analyses on the yield loss-weed density function. The model performs gross margin analysis (see equations 3-16, SI) and incorporates the effect of variables such as soil type, sowing date, tillage practices and yield penalties associated with crop sequences. This allows us to estimate the costs associated with a range of management practices aimed at reducing BG populations. It is built in R[45] and uses a simple data-entry system. For further details see SI and Code Availability statement.

The baseline for this analysis was harvest 2014 because this was the first year in which we undertook field surveys of BG density and crop yield. All costings were therefore made using 2014 prices[46,47] (e.g. we assumed a wheat price of £164 t^{-1}, which was the average for feed wheat (£155 t^{-1}) and milling wheat (£173 t^{-1}) in 2014). Prices given on GitHub, see Data Availability statement. For herbicide prices we calculated mean values from our dataset: selective herbicides targeting black-grass = £19.50 l^{-1}, glyphosate = £2.43 l^{-1}. Estimates of the cost of resistance will vary, potentially greatly, as input prices (especially herbicide) and output prices (especially winter wheat) change each year.

The model can be run for multiple fields and years. This makes it useful for estimating economic impacts of current and historical weed infestations, for working with very large datasets – thereby enabling more reliable up-scaling to policy-relevant scales – and for aiding within-year decision-making at the field scale or multi-year planning at a farm or landscape scale.

Estimating yield loss due to black-grass. High-resolution yield data, available for 17 fields from years 2014-2017 (Supplementary Figure 1), were used to estimate the BG density-wheat yield relationship (Figure 1, Supplementary Table 1) using a mixed effects model fitted using the lmer() function in the lme4 library[48] in R[45] (model details in Supplementary Methods and Supplementary Figure 2). From this model we predicted mean yield at each density state in an 'average' field (Figure 1a and Supplementary Table 2). Parametric bootstrap 95% confidence intervals around these means were estimated from 10,000 re-samples[49] from the model posterior with the 'bootMer()' function from lme4. We calculated the percent reduction in yield (Figure 1b) from the reference state ('low') for the other three density states using 1 – (predicted yield for state D / reference state yield). These estimates of yield loss are in line with published yield losses due to BG in controlled plot experiments (Supplementary Table 3). We generated 95% confidence intervals on the percent reduction (used to inform limits in sensitivity analyses) by calculating the percent reduction for each density state for each of the 10,000 bootstrap samples, then taking the 95% quantiles of those distributions of estimated percent reductions. The resultant yield penalties applied in BGRI-ECOMOD are given in Supplementary Table 2. Further methodological details in SI.

Estimating field-scale C_R and YL_R. Our aim was to estimate the average cost and yield loss per hectare for different densities of resistant BG at a baseline point in time (2014, see above). Costs were calculated using 2014 prices (and so will differ if using prices from other years).

Stage 1 was to estimate costs and yield losses due to BG infestation (*I*). First, we derived a yield penalty for each weed density state as described above and applied them as parameters in BGRI-ECOMOD. We then ran the historical field management data and BG density data from the 66 fields through BGRI-ECOMOD to estimate (a) yield loss due to BG infestation (YL_I), and (b) costs due to yield loss and herbicide application (chemical + operations costs) resulting from BG infestation (C_I), for every field in every year (maximum date range 2004 – 2014). We did this by running the model both *with* and *without* BG infestation, then subtracting the estimated gross profit or yield obtained in the presence of BG from that estimated in the absence of BG (*i.e.* the potential profit or yield).

For wheat, running the model *with* BG infestation involved four model runs because different BG density states resulted in different wheat yield penalties, so we had to run our field management history through the model once for each density state: *i.e.* in subsequent model runs, BG density for all fields was set at absent/low, then medium, then high and then very high states, each time using the observed herbicide and spraying data. For each field we then calculated mean gross profit and yield weighted by the proportion of each density state in the field (see Supplementary Figure 3). Finally, the model was run *without* BG infestation, so the density state of all fields was set to absent/low and herbicide applications and spraying operations targeting BG were set to zero. The weighted mean gross profit (or yield) was then subtracted from the potential profit (or yield) to give a cost and yield loss due to BG infestation in winter wheat crops for each field. For other crops the process was simpler as BG density and yield were not surveyed. Therefore, to estimate C_I across all crops (which, for any given field, is effectively C_I across a rotation), the model was run only twice, *with* and *without* BG infestation, and then the calculated costs were averaged over the number of year's management history for each field, giving a mean rotation C_I for each field.

Stage 2 was the estimation of costs and yield losses due to resistant (*R*) plants. For each field, the frequency of resistance to mesosulfuron was then used to calculate the proportion of the costs or yield losses that were due to *R* plants, giving a cost of resistance (C_R) and yield loss due to resistance (YL_R). We chose the frequency of resistance to mesosulfuron because, of three actives tested, mesosulfuron (an ALS inhibitor) was the strongest driver of BG abundance in our fields in 2014 (Comont et al, in prep). Furthermore, ALS target-site resistance was identified as a particular concern back in 2007[26].

Using these field-scale estimates, for both winter wheat crops and rotations, we derived an average C_R and YL_R per hectare for each of the four weed density states. This was our baseline C_R and YL_R. Further methodological details given in Supplementary Figure 3.

To estimate the worst-case scenario in winter wheat crops (*i.e.* cost and yield loss under a total loss of herbicide control), we used the methodology described in (ii) above but assumed in the second model run that all quadrats in every field were in a very high density state. Because at very high density 100% of costs and yield losses were due to resistant plants, we assumed 100% of costs and yield loss were due to resistance. Herbicide applications remained unchanged – *i.e.* we used the herbicide application data from the management history – although, in reality, where black-grass was initially absent herbicide applications would have been likely to increase. The resulting per hectare costs differ very slightly to those calculated previously for very high density states because the management history data of all fields was used in this worst case estimate, rather than the data from just those fields with very high average density states. We also made two more-conservative estimates of a worst-case scenario by scaling up the average costs and yield losses from fields in the top decile and top quintile of observed black-grass density states.

The relative contribution of herbicide application, yield loss and operations costs to overall cost in winter wheat crops (Figure 3) was assessed by extracting individual components from ECOMOD output (output generated by running empirical field management data from 66 fields through ECOMOD, as described above). The effect of weed density on herbicide use in winter wheat crops was assessed using a generalized linear mixed effects model and performing a likelihood ratio test using maximum-likelihood simplification of the minimal adequate REML model. The model was fit with the lmer function in package lme4[48] and included farm as a random effect to account for multiple fields on the same farm. Model fit was assessed by visual inspection of residual plots, which indicated no signs of heteroscedasticity or non-normality.

Scaling-up the cost of resistance. Fields were chosen to be representative of UK arable farming. Farms were predominantly arable, the geographic range (Oxfordshire to Yorkshire) encompassed the main winter wheat-growing areas of the UK, and a range of farm sizes was included. Within farms, field selection was based on those that were in winter wheat in the first survey year. Farmers were asked to select their 'best' and 'worst' fields in terms of BG infestation. We therefore assumed fields to be representative of both arable farming and BG resistance and density distributions within our wider study area and in England as a whole (evidence for which can be seen in the fact that ECOMOD provides similar gross profit estimates to those in the Farm Business Survey[50], Supplementary Table 4). We scaled up the costs of resistance accordingly.

C_R and YL_R in winter wheat were scaled up to regional winter wheat areas (DEFRA, 2014). For each region, we estimated the area of wheat at each BG density state by taking the proportion of that region's surveyed fields at each density state, then multiplying the regional wheat area by these proportions (Supplementary Figure 3; all 138 fields in the dataset were used in this process). Next, for each density state and region, these wheat cropping areas were used to scale up the per hectare C_R and YL_R (Supplementary Methods, equation (1)). For each region, costs for each density state were summed to give a regional total (Supplementary Methods, equation (2)). This methodology ensures that the up-scaling of costs and yield losses in winter wheat better reflects regional differences in BG density[1]. The costs across rotations were scaled up directly to regional cereal cropping areas (DEFRA, 2014) as we have no data on BG density in crops other than wheat. Further details in Supplementary Methods.

Assumptions. We assume that the herbicide resistant BG phenotype is present in every field, based on previous work[1] which found that only 1% of fields in our dataset had no resistance to any of the three herbicides tested. Furthermore, of the 126 fields from our dataset with the best-quality phenotyping data (these include Northern fields, where resistance is less of a problem), only 1 field had <10% survival when Fenoxaprop was applied at field rate. We are thus confident that that there is some level of herbicide survival in almost every field. In terms of the effect of herbicide, we assume that resistant (*R*) plants survive a field-relevant dose of herbicide. At the individual scale this means that R is binary (0|1) after herbicide. At the population scale it is more continuous (0-1): herbicide reduces BG abundance by the proportion of susceptible (S) individuals.

We assume that herbicide does not drive the BG seedbank to zero before the field evolves resistance. Weed eradication using herbicide alone is almost always impossible due to spatial and temporal refuges from herbicide treatments (e.g. field margins, seed bank, asynchronous germination, and transfer of weed seed between fields on machinery), so there are almost inevitably herbicide ‘escapes’ capable of maintaining a population. More broadly, feasibility studies of general weed eradication programmes have highlighted the concerted and prolonged effort required for eradication to be successful[51]. Despite relatively small field sizes, this degree of effort is unlikely to be met for most farms, particularly using herbicide alone.

We assume that the resistant BG phenotype has the same impact on yield as the susceptible wildtype. There is good evidence illustrating how limited the effects of both non-target-site resistance (NTSR) and some predominant target-site resistance (TSR) mutations are on relative performance of R and S BG biotypes[52–54], and thus any influence on competition with the crop is likely to be negligible. Comparisons of NTSR and susceptible BG found no consistent fitness costs, either when grown alone or in competition with winter wheat[52,54]. In a study of three ACCase TSR mutations in BG[53], one mutant allele (Gly-2078) did result in a small reduction in biomass and seed production; however, this mutation is rare, with a frequency of only 0.34% based on previous genotyping of 8256 haplotypes from UK BG[55]. Additionally, there is some evidence that the small fitness costs associated with this mutation are rapidly lost in BG populations due to compensatory evolution[56]. Two mutations (Leu 1781 and Asn-2041), which are considerably more common in UK BG[55], had no effect on vegetative biomass, height or seed production compared to S wild-type plants. We are thus confident in our assumption that R phenotypes of BG have the same impact on yield as the S wild-type.

To calculate C_R across the time span of our dataset (2004 – 2014) we assumed that the density state of a field as recorded in 2014 also applied to all the preceding years for which we had management history data (we had no density data pre-2014). Hicks et al[1] found slight evidence for a within-field increase in density between 2014 and 2016, and showed that resistance is driving black-grass density. However, this increase in density is not at a magnitude to change the categorical density state of a field unless over a fairly long timescale and could well simply represent normal inter-annual fluctuations. To test the validity of using the entire time span, we re-ran the analysis on just the later part of the time series (2010 – 2014 inclusive). Although this gave slightly higher costs (Supplementary Table 9), the costs estimated using 2010 – 2014 data fell within the 95% CIs estimated using 2004 – 2014 data, indicating that the assumption holds here.

To estimate the worst-case scenario in winter wheat crops, we assumed all quadrats in every field were at very high density state and that resistant plants were responsible for 100% of costs and yield losses. This scenario would arise only if no action were taken to address current problems of herbicide resistance and assumes that farmers keep applying herbicide even once its efficacy is limited. Although there is evidence for these types of behaviours[1,57,58], this scenario is not currently anticipated and we present it only to highlight the worst possible effects of inaction.

Model testing and evaluation. Model tests were carried out on yield and gross margin. For evaluation of yield estimates, we first removed from the dataset any observations (n =13) where a farmer grew a crop not modelled by BGRI-ECOMOD. The model accurately estimated yield both with (R^2=0.91, slope=1.05, Supplementary Figure 4) and without (R^2=0.97, slope=1.05, Supplementary Figure 4) failed crops in the dataset (BGRI-ECOMOD is unable to predict crop failure). We also evaluated yield estimates without the heavy crops (potatoes, sugar beet) to remove their influence on the relationship: the model still estimated yield well (R^2=0.74, slope=1.01). Estimated regional gross margin fell within the 95% confidence intervals for the regional values obtained from Farm Business Survey data (Supplementary Table 4). Furthermore, the model was robust to sensitivity testing on tractor work rates during different tillage operations, which was the management variable for which published data were lacking. We varied the proportions used to calculate tillage work rates in relation to ploughing work rate: the range tested was +30% to -30% (+/-5%, +/-10%, +/-20% and +/-30%) of initial values. There was no effect on the per hectare C_R (results not shown).

The model was, however, sensitive to the yield penalty applied for BG infestation. We observed considerable variability in the yield loss~weed density relationship (Supplementary Figure 1), especially at the highest density, and so ran a sensitivity analysis based on the extremes from our data and the literature (Supplementary Table 10). The consequences of using different yield penalties are given in the results and in Supplementary Table 11. Full details of model tests and sensitivity analyses are given in Supplementary Methods.

Data availability

Model data and input template are available at https://github.com/alexavarah/BGRI-ECOMOD. Data used to generate the yield penalty can be accessed at https://github.com/alexavarah/BGcosts. The field management data set has been deposited in the University of Sheffield Online Research data archive (ORDA) and can be accessed at https://figshare.com/s/eb21f4d1862741d50ceb.

Code availability

Model code is available at https://github.com/alexavarah/BGRI-ECOMOD.

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Acknowledgements

The authors thank the farmers who allowed their fields to be surveyed and provided field management data. This work was funded by BBSRC (BB/L001489/1) and the Agriculture and Horticulture Development Board (Cereals and Oilseeds).

Author contributions

Data were collected by H.L.H., D.C., L.C. and R.H.. BGRI-ECOMOD was designed by A.V. and K.A. and built by K.A.. A.V. did all analysis. S.R.C. and D.C. generated the yield penalty estimates and associated figures, and S.R.C. contributed to sensitivity analysis work. R.P.F. contributed the density map in Figure 2. A.V. drafted the initial manuscript and H.L.H, D.C., S.R.C, P.N., D.Z.C., R.P.F., K.N. contributed to refining it. Funding was acquired by R.P.F., D.Z.C., P.N. and K.N.

Competing interests

A.V., K.W., H.L.H., D.C., S.R.C., L.C., R.H., D.Z.C., R.P.F., K.N. declare they have no competing financial interests; P.N. supervises a PhD student co-funded by Bayer (not part of this project).

Figure legends

Fig. 1 | Estimating yield penalties using black-grass density and winter wheat yield data. a, The average effect of black-grass density on the yield of winter wheat. Black points are model-estimated average yields, bars show 95% confidence intervals generated from 10,000 parametric bootstrap re-samples (some confidence intervals are narrow enough to be obscured by the point; all values and confidence intervals given in Supplementary Table 2). Grey points show observed yield for each 20 x 20 m plot from 17 fields over 4 years. See SI for individual field estimates across years. **b,** Average yield loss of winter wheat relative to the reference state, calculated based on yield estimates and bootstrap resamples. Reference state = low density (note the estimate for low density is fixed at 0). Percent reduction for subsequent density states as follows: medium 0 %; high 7.45 %; very high 25.60 % (Supplementary Table 2). The y-axis of (**b**) is reversed so that the direction of the effect of black-grass density is the same between (**a**) and (**b**). Further details in SI.

Fig. 2 | Field-scale costs and yield loss due to resistant black-grass. These estimates were generated by running empirical field management and black-grass density data (number of fields = 66) through BGRI-ECOMOD. **a** and **b** show yield loss due to resistant black-grass (YL_R, t ha^{-1}): **a,** average field-scale yield losses in winter wheat; **b,** maximum field-scale yield loss in winter wheat in the event of total loss of herbicide control. **c – e** show cost of resistance (C_R, £ ha^{-1}): average field-scale C_R for **c,** years in winter wheat crops and **d,** all years' data, *i.e.* across a rotation; **e,** maximum field-scale C_R in the event of total loss of herbicide control. Fields are overlaid on a map of modelled density (square root) of *Alopecurus myosuroides* averaged over 2015-2017. This density map was generated by fitting a generalized additive model to the data reported in Hicks et al. (2018)[1], with spatial covariates representing latitude and longitude.

Fig. 3 | The relative contribution of herbicide costs, lost yield and operations costs to total costs in winter wheat crops. Values are average per hectare costs estimated by running empirical field management and black-grass density data through BGRI-ECOMOD (number of fields = 66). **a,** Costs due to resistant black-grass plants and **b,** costs due to infestation. Herbicide costs consider only those herbicide applications targeting black-grass. (Error bars intentionally omitted as the purpose is to illustrate the contribution of component parts and, when data are presented in this way, error bars of individual components influence each other and are misleading).

Fig. 4 | Annual impacts of herbicide resistant black-grass at regional and national scales. a, Annual winter wheat yield losses due to resistance (YL_R). National YL_R given in million tonnes; regional figures in thousand tonnes. **b,** Annual economic cost of resistance (C_R) across all crops and **c,** in winter wheat crops. National C_R in billion GBP, regional C_R in million GBP. Figures in brackets are 95% confidence intervals. Regions are UK Government Office regions: EE East of England; SE South East; YH Yorkshire and the Humber; EM East Midlands; WM West Midlands. For each region, the mean per hectare C_R and YL_R at each black-grass density state were multiplied by the crop area estimated to have that density state. For full details of scaling-up process see Methods and SI.

Tables

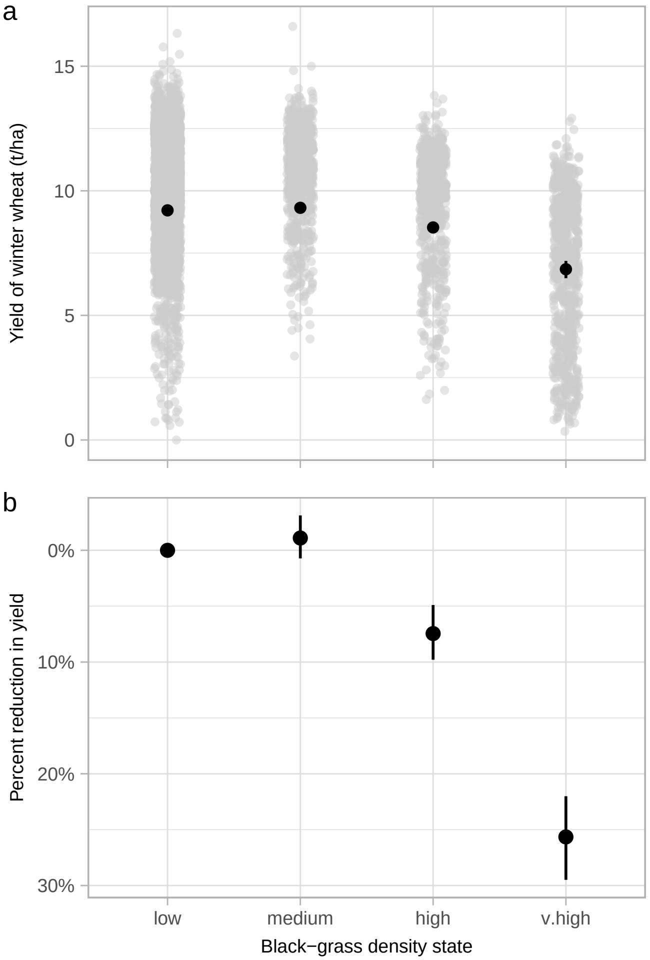
Table 1 | Field-scale yield loss and economic costs due to black-grass infestation (*I*) and resistant plants (*R*) at different densities of black-grass in England.

Average black-grass density state of field	**Average yield loss in winter wheat[†] (t /ha)**			**Average cost[†] (£ /ha)**					
				in winter wheat			**across rotations**		
	R	*I*[*]	*R/I*[◇]	*R*	*I*	*R/I*	*R*	*I*	*R/I*
absent/low	0.0 (-0.1, 0.1)	0.0 (-0.1, 0.1)	NA	75 (56, 93)	106 (90, 123)	0.71	58 (44, 72)	85 (73, 98)	0.68
medium	0.3 (0.2, 0.4)	0.4 (0.2, 0.4)	0.75	135 (120, 149)	158 (148, 168)	0.85	103 (91, 115)	123 (114, 132)	0.84
high	0.8 (0.7, 0.9)	0.9 (0.8, 1.0)	0.89	264 (249, 280)	276 (261, 291)	0.96	185 (173, 197)	193 (182, 204)	0.96
very high	1.8 (1.7, 1.9)	1.8 (1.7, 1.9)	1.00	450 (434, 466)	450 (434, 466)	1.00	280 (263, 297)	280 (263, 297)	1.00
Mean across all densities	0.38 (0.2, 0.6)	0.41 (0.2, 0.6)	0.93	155 (135, 174)	178 (152, 204)	0.87	112 (92, 132)	131 (114, 148)	0.85

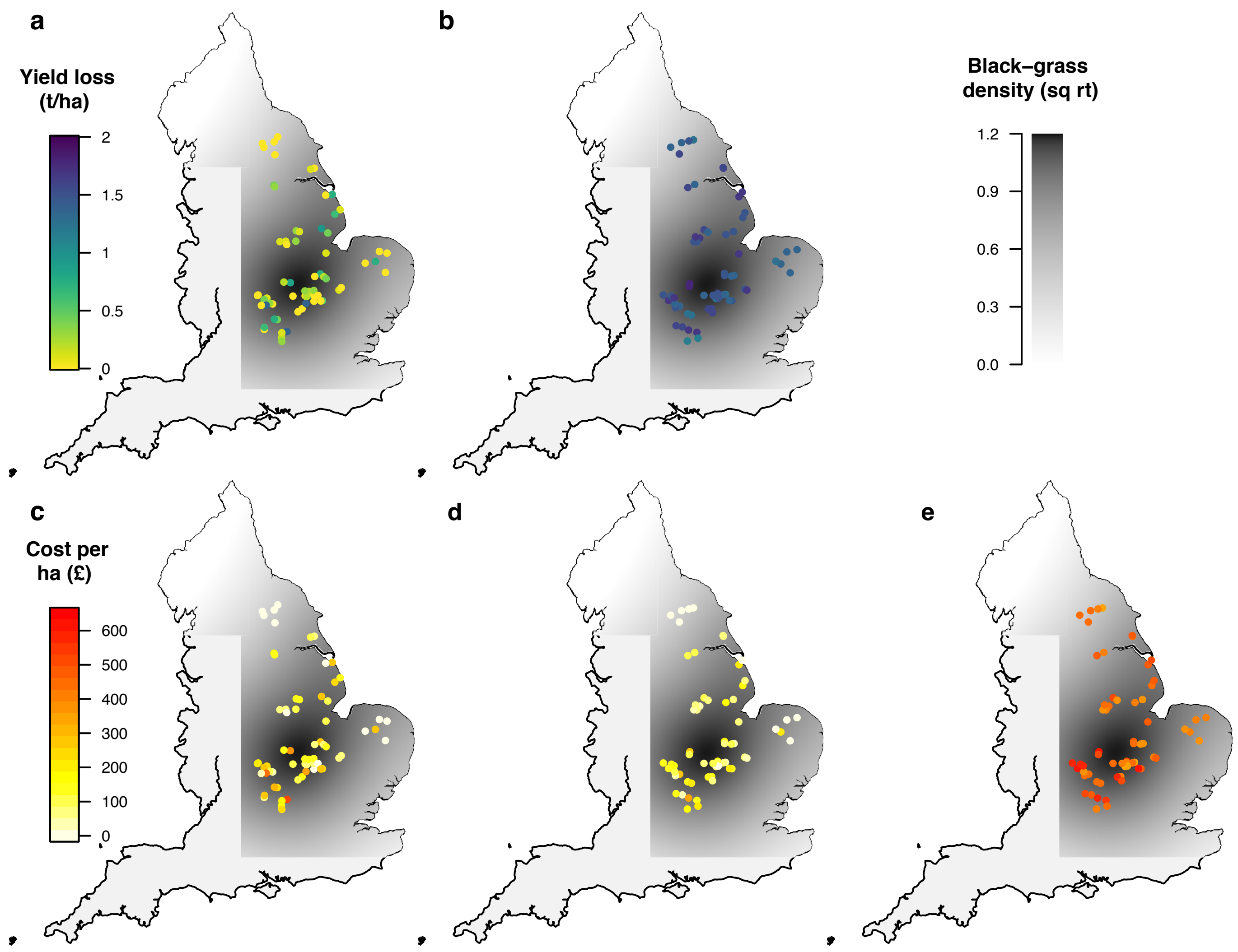
[†] Values are means, estimated by running empirical field management and black-grass density data (number of fields = 66) through BGRI-ECOMOD, see Methods. 95% confidence intervals (generated by bootstrapping) in brackets.

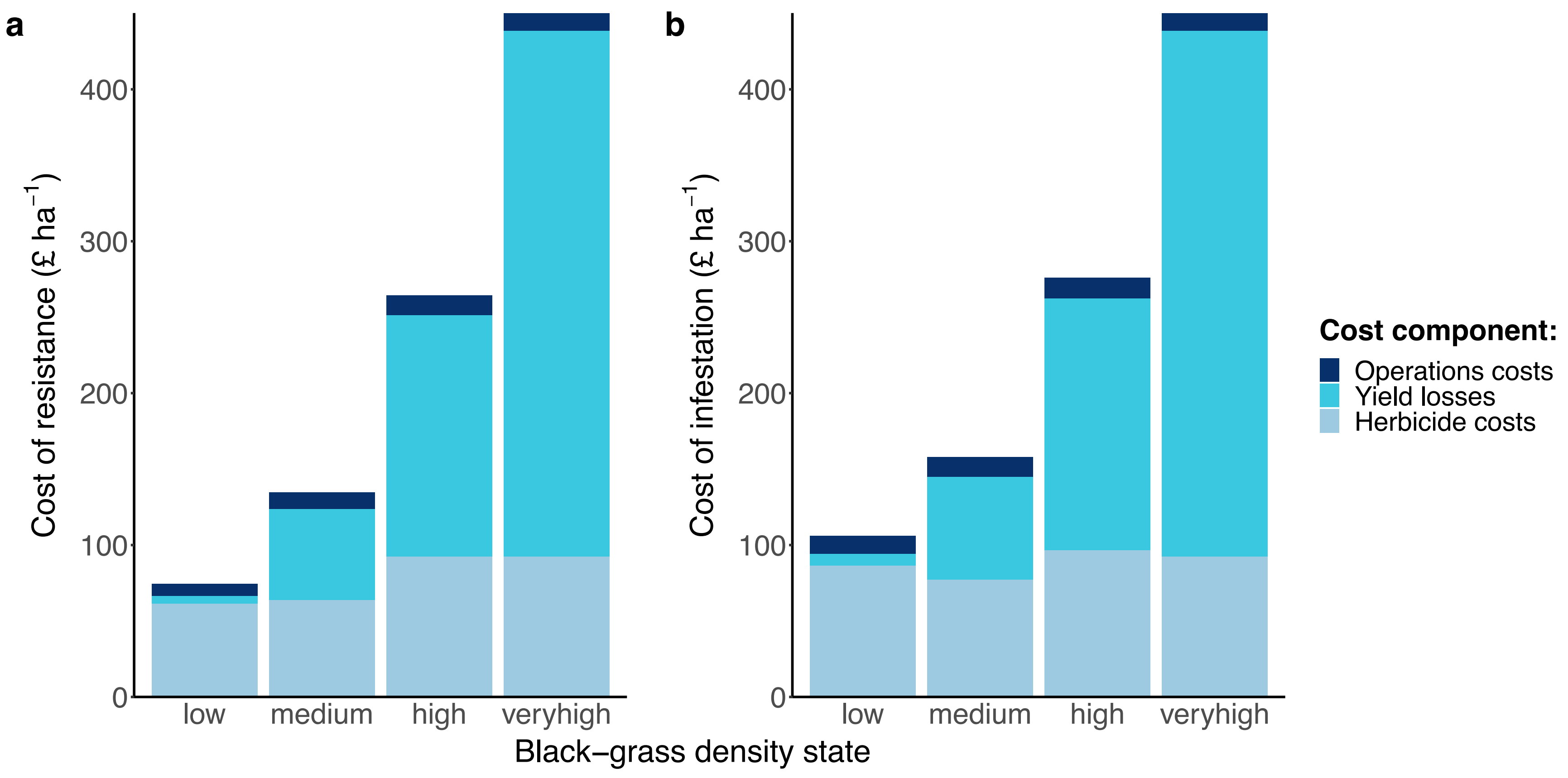
[◇] *R/I* gives the proportion of the cost of infestation that is due to resistance.

[*] infestation = resistant + susceptible plants.

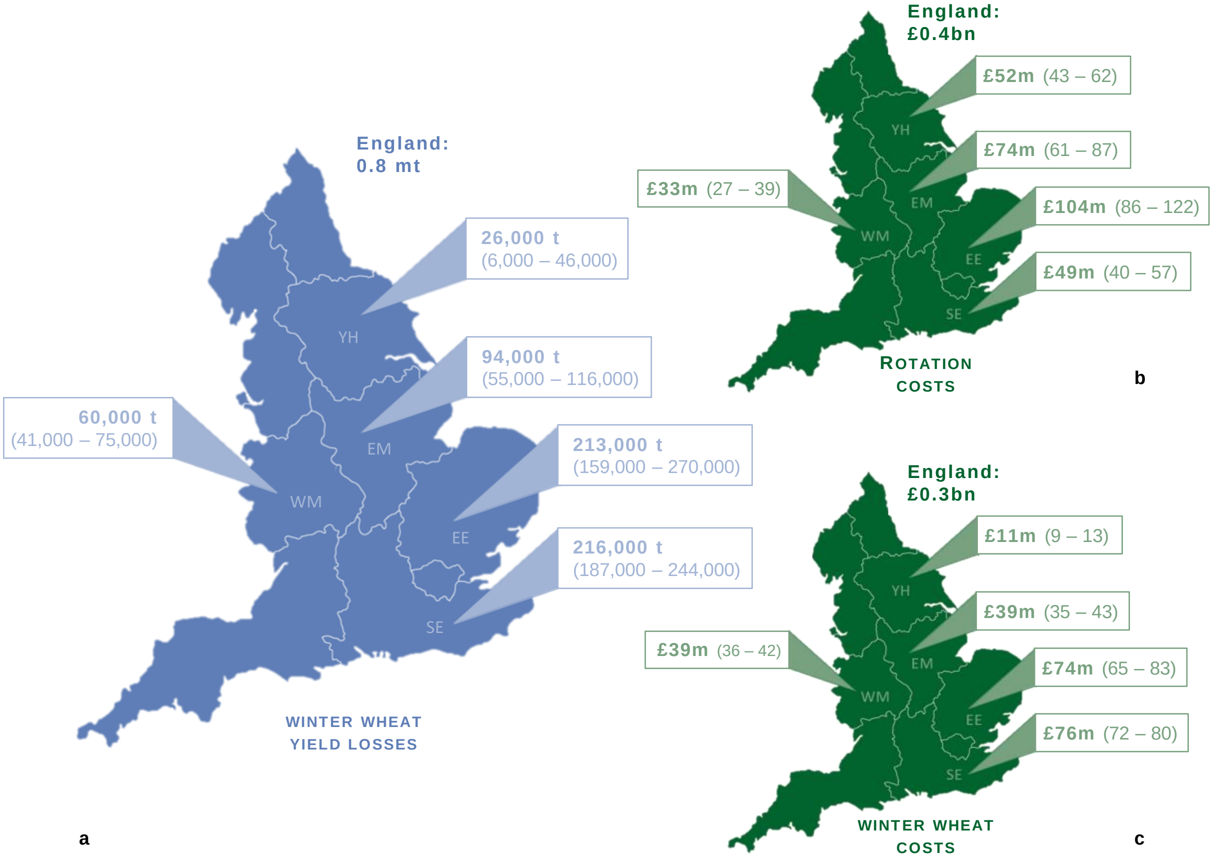


a
Yield of winter wheat (t/ha)
0
5
10
15
b
Percent reduction in yield
0%
10%
20%
30%
low
medium
high
v.high
Black−grass density state


a
Yield loss
(t/ha)
2
1.5
1
0.5
0
b
Black–grass
density (sq rt)
1.2
0.9
0.6
0.3
0.0
c
Cost per
ha (£)
600
500
400
300
200
100
0
d
e



a
b
Cost of resistance (£ ha^{-1})
Cost of infestation (£ ha^{-1})
0
100
200
300
400
low
medium
high
veryhigh
Black–grass density state
Cost component:
Operations costs
Yield losses
Herbicide costs


England:
0.8 mt
26,000 t
(6,000 – 46,000)
94,000 t
(55,000 – 116,000)
60,000 t
(41,000 – 75,000)
213,000 t
(159,000 – 270,000)
216,000 t
(187,000 – 244,000)
YH
EM
WM
EE
SE
WINTER WHEAT
YIELD LOSSES
a
England:
£0.4bn
£52m (43 – 62)
£74m (61 – 87)
£33m (27 – 39)
£104m (86 – 122)
£49m (40 – 57)
ROTATION
COSTS
b
England:
£0.3bn
£11m (9 – 13)
£39m (35 – 43)
£39m (36 – 42)
£74m (65 – 83)
£76m (72 – 80)
WINTER WHEAT
COSTS
c