

A process-based approach to modelling impacts of climate change on the damage niche of an agricultural weed

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Abstract

Predicting the impact of climate change on the damage niche of an agricultural weed at a local scale requires a process-based modelling approach that integrates local environmental conditions and the differential responses of the crop and weed to change. A simulation model of the growth and population dynamics of winter wheat and a competing weed, Sirius 2010, was calibrated and validated for the most economically damaging weed in UK cereals, *Alopecurus myosuroides*. The model was run using local-scale climatic scenarios generated by the LARS-WG weather generator and based on the HadCM3 projections for the periods 2046–2065 and 2080–2099 to predict the impact of climate change on the population dynamics of the weed and its effect on wheat yields. Owing to rising CO₂ concentration and its effect on radiation use efficiency of wheat, weed-free wheat yields were predicted to increase. The distribution of the weed was predicted to remain broadly similar with a possible northward shift in range. Local-scale variation in the impact of climate change was apparent owing to variation in soil type and water holding capacity. The competitive balance was shifted in favour of the deeper rooted crop under climate change, particularly on sites with lighter soils, owing to more frequent and severe drought stress events. Although the damage niche of *A. myosuroides* was predicted to reduce under climate change, it is likely that weeds with contrasting physiology, such as C4 species, will be better adapted to future conditions and pose a more serious threat.

Keywords: *Alopecurus myosuroides*, drought stress, resource competition, Sirius 2010, winter wheat

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Introduction

Modelling the impact of climate change on the geographical range of a species and its potential to invade new habitats will require a hierarchical, interdisciplinary approach (Pearson *et al.*, 2004; Bradley *et al.*, 2010; Kueffer, 2010). The method used to model a system, from correlative or bioclimatic envelope models (also known as species distribution or niche-based models) to complex, mechanistic process-based models, will be dependent on scale and, where appropriate, will require integrated approaches (Morin & Thuiller, 2009). Underlying this challenge is the fact that the number of drivers that need to be incorporated into models of biological community assembly increase as scale decreases. At global or continental scales, climatic variables can be assumed to be the primary drivers, but at the regional or local scales, site-specific environmental, management or biological variables become increasingly important (Pearson & Dawson, 2003). Although bioclimatic envelope models are a useful first approxi-

mation to the present and future range of a species, they are open to criticism when applied at smaller scales because they do not account for barriers to dispersal, local soil or management factors, biotic interactions and the capacity of species to adapt to new environments (Davis *et al.*, 1998, 2005; Thuiller *et al.*, 2008). Modelling these multiple factors, however, requires a process-based approach with the associated demands on data collection and model parameterization – a challenge previously described as the tractability/complexity trade-off (Thuiller *et al.*, 2008).

Climate change is anticipated to have important implications for agricultural productivity (Howden *et al.*, 2007; Jaggard *et al.*, 2010). Among the factors that may be affected are the incidence of pests and diseases. Predicting shifts in the distribution and impact of agricultural weeds under climate change will, therefore, be an important consideration in designing strategies for adaptation (Patterson, 1995; McDonald *et al.*, 2009; Clements & Ditommaso, 2011). In addition to the economic importance of quantifying the impact of climate change on yield loss from weeds, the arable system also represents an ideal system for developing the integrated modelling approach to predicting the

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response of plant communities discussed above. Because the cropped field is highly regulated through management, modelling the biological processes is more tractable, and there is the potential to address the limitations that currently hinder the application of process-based models to predicting the impact of climate change on plant communities at a regional or local scale. First, in contrast to semi-natural habitats that are characterized by a complex web of biotic interactions between multiple plant and animal species (Araujo & Luoto, 2007), arable fields are dominated by a single crop species with a small number of competing weeds, and herbivore pressure is minimized by the use of pesticides. The complexity of modelling the impact of climate change on biotic interactions is, therefore, reduced to the relatively simple challenge of quantifying changes in crop-weed competitive dynamics in response to climatic perturbations. A number of process-based, weather-driven models have recently been validated that predict the impact of weeds on crop yield and the concomitant effects on weed biomass and population dynamics (Kropff & Spitters, 1992; Debaeke *et al.*, 1997; Deen *et al.*, 2003). These models have primarily been developed as an agronomic tool, but the extensive experimental work that has been done to quantify the required eco-physiological parameters makes them ideally suited to predict the response of weeds to climate change at the regional or local scale. The concurrent independent development of crop simulation models, which have been used to investigate the impact of climate change on crop growth, development and yield (Semenov *et al.*, 1996; Jamieson *et al.*, 2000; Ewert *et al.*, 2002; Semenov, 2009; Semenov & Shewry, 2011), also means that the biological context for modelling weed dynamics is well parameterized.

A second challenge to the development of process-based models of the response of plant communities to climate change is the complexity of spatial dynamics. Bioclimatic envelope models generally assume no or unlimited migration and are, therefore, unable to account for limited dispersal abilities or barriers to range expansion due to, for example, habitat fragmentation (Collingham *et al.*, 2000; Thuiller *et al.*, 2008). Again, to incorporate dispersal into a mechanistic, spatially explicit model within a heterogeneous landscape requires a substantial input of data on demographic processes many of which may be unavailable (Thuiller *et al.*, 2008). Arable systems have a number of advantages which make this problem of accounting for spatially dependent processes tractable. First, agricultural weeds are characterized by a ruderal ecological strategy. They are usually small seeded, fecund and fast growing. This makes them well adapted to widespread dispersal to take advantage of ephemeral habitats that may be

created by disturbance. Weed seeds are also regularly transported between localities on farm machinery, further aiding the spread of weeds in the landscape (Hunston *et al.*, 2005). Second, agricultural landscapes are relatively simple with large contiguous areas of cultivated land resulting in a continuity of suitable habitat for weeds. It is, therefore, reasonable to assume that on a regional or local scale, any newly available niche will be colonized well within the time-scale within which climate change scenarios are generally framed.

In this paper, we demonstrate the potential for modelling the impact of climate change on the distribution of agricultural weeds and consequent crop yield loss (or damage niche) using *Alopecurus myosuroides* Huds. (black-grass) in winter wheat (*Triticum aestivum* L.) as a model system. *Alopecurus myosuroides* is among the most economically important weeds in terms of yield losses incurred in western European cereal production and is becoming increasingly problematic because of the development of resistance to a number of herbicide groups (Moss *et al.*, 2007). Within the United Kingdom, the species is largely confined to cereal growing areas in the south and east of the country with a clear northern limit to its current distribution (Preston *et al.*, 2002; Fig. 1). *Alopecurus myosuroides* has been the focus of extensive applied research, and a number of models, of varying complexity, have been developed to predict its competition with the crop and population dynamics (Moss, 1985; Storkey *et al.*, 2003; Colbach *et al.*, 2007). We combined published algorithms for modelling the impact of weather and the environment on different stages of the weed life cycle and inter-plant competition (Kropff & Spitters, 1992) with a process-based model of crop growth and development (Jamieson *et al.*, 1998) drawing on experimental data across multiple years and sites to calibrate and validate the final model. The model is applied to the United Kingdom using regional data on soil properties and local-scale climate scenarios derived from a stochastic weather generator (WG) and based on climate projection from the Met. Office Hadley Centre Global Climate Model (HadCM3) (Semenov & Stratonovitch, 2010; Semenov *et al.*, 2010). In so doing, we predict the shift in the realized niche for *A. myosuroides* in the United Kingdom in terms of population growth rates (λ) and the expected crop yield loss or 'damage niche' of the weed (*sensu* McDonald *et al.*, 2009).

Materials and methods

Modelling plant growth and competition for light, water and nutrients

Sirius 2010 is a crop simulation model capable of modelling inter-plant competition for light, water and nutrients and crop

yield. It is based on the original Sirius wheat model (Jamieson *et al.*, 1998; Jamieson & Semenov, 2000; Lawless *et al.*, 2005) with elements of the INTERCOM model of crop-weed competition (Kropff & Spitters, 1992). Sirius 2010 simulates plant growth and development at a daily time-scale within a uniform field. Plants of different species are described as a collection of organs (roots, leaves, stems, flowers and seeds) collectively competing for light, water and nitrogen. A single cohort represents all individual of the same species germinated at the same time.

The canopy consists of leaves, stems and flowers from all cohorts. Each of these organs has a vertical position within the canopy (offset from ground) and is described by different light characteristics (e.g. light extinction coefficient). Light is intercepted by the canopy following a Beer-Lambert law. To account for light competition, the canopy is split vertically in thin layers of size cls (5 cm). The light absorbance of the organ o , in the layer l of the canopy is related to the organ light extinction coefficient (kl , dimensionless) and the organ area density (ad , m^{-1}) in this layer:

$$a(l, o) = kl(o) \times ad(l, o) \times cls.$$

The entire canopy absorbance in this layer l is

$$a(l) = \sum_{c=1}^{nc} \sum_{o=1}^{no(c)} a(l, o),$$

where nc is the number of cohort and $no(c)$ is the number of organ of the cohort c .

Radiation (r , $MJ m^{-2}$) intercepted by the canopy in the layer l is calculated from the daily photosynthetically active radiation (par , $MJ m^{-2}$):

$$r(l) = par \times (e^{-\sum_{m=1}^{nl} a(m)} - e^{-\sum_{m=l+1}^{nl} a(m)}),$$

where nl is the number of canopy layer.

The amount of radiation absorbed by the organ o in the layer l is related to its absorbance:

$$r(l, o) = r(l) \times \frac{a(l, o)}{a(l)}.$$

The total amount of radiation absorbed by the organ o is the sum of radiation absorbed in each layer where the organ is present:

$$r(o) = \sum_{l=bl(o)}^{tl(o)} r(l, o),$$

where $bl(o)$ and $tl(o)$ are, respectively, the index of the bottom and top layer of the organ o .

We calculated daily potential dry mass assimilation by an organ (pa , g (DM)) using the daily radiation use efficiency (rue , g (DM) $MJ^{-1} m^2$):

$$pa(o) = r(o) \times rue(o).$$

Radiation use efficiency incorporated the plant assimilation responses to daily and global environmental variables and was affected by atmospheric CO_2 concentration (f_{CO_2} , dimensionless), temperatures (f_T dimensionless) and water stress

(f_W , dimensionless):

$$rue(o) = lue(o) \times f_{CO_2} \times f_T \times f_W,$$

where f_{CO_2} increases with atmospheric CO_2 concentration ($[CO_2]$ ppm) by 30% for a doubling of $[CO_2]$ compared with the baseline $[CO_2]$ of 350 ppm:

$$f_{CO_2} = 1 + 0.3 \times \frac{[CO_2] - 350}{350}.$$

A similar response has been used by other wheat simulation models e.g. CERES (Jamieson *et al.*, 2000) and EPIC (Tubiello *et al.*, 2000). The temperature and water stress responses are calculated as in Ewert *et al.* (2002). Competition for soil resources is handled from top to bottom, splitting soil layer resources between cohorts according to their demand. At the soil layer l , the amount of resources demanded by the cohort c is

$$d(l, c) = d(c) - \sum_{i=1}^{l-1} u(i, c),$$

where $d(c)$ is the daily total demand of the cohort c , $u(i, c)$ is the uptake of cohort c on the soil layer i . The amount of resources received by the cohort c from the soil layer l when nc cohort are competing is proportional to its demand:

$$u(l, c) = \begin{cases} 0, & d(l, c) = 0 \\ \frac{d(l, c)}{\sum_{i=1}^{nc} d(l, i)} \times d(l, c), & d(l, c) > 0 \end{cases}$$

The total amount of resources obtained by the cohort c on from the soil is

$$u(c) = \sum_{l=1}^{nsl(c)} u(l, c),$$

where $nsl(c)$ is the number of soil layer accessible by the cohort c .

Experimental data for model calibration and validation

The model parameters were calibrated using data collected as part of a series of experiments done at Rothamsted Research (Hertfordshire, UK) to measure the eco-physiological traits of a range of UK weeds (Storkey, 2006). *Alopecurus myosuroides* populations were broadcast by hand into small experimental plots (3 × 3 m) immediately prior to a crop of winter wheat being drilled at 300 seeds m^{-2} . The weed was thinned to 50 plants m^{-2} in a central 1 m^2 area at the centre of each plot. There were three replicate plots and the experiment was repeated in 3 years with the following sowing dates: 27 September 2001, 17 October 2002 and 29 September 2004. In each year, at intervals of approximately 4 weeks, five plants per plot were sampled and divided into leaf, stem and heads. Leaf and stem area was measured using a Delta-T WinDias leaf area metre (Cambridgeshire, UK) and the separate plant parts dried for 24 h at 80 °C and weighed. At each sampling date, the height of the five individual weed plants was also measured. The time of first flowering was recorded from regular field visits.

A separate dataset of crop/weed competition measured at six sites in the United Kingdom over 3 years was used to

validate the model. The experiment sites represented a range of soil types (Table S1, Supporting Information) and the experiments were carried out in the seasons 1994/1995, 1995/1996 and 1996/1997 – the site at Woburn was only used in the first year. All experiments were of a randomized block design with three replicates. The experimental sites were cultivated using best local practice to produce good seed-beds, and the plots were sown at the very end of September or in October (Table S1, Supporting Information). Six different densities of *A. myosuroides* were broadcast by hand onto the plots immediately prior to a crop of winter wheat being drilled; target weed densities were 0, 40, 80, 160, 320, 640 plants m⁻². Plot sizes varied to fit in with the local farm practice but were typically 24 m². The density of weed and crop seedlings was assessed after establishment in the autumn by counting the number of weed plants in ten 0.25 m⁻² quadrats per plot. Crop density was assessed by counting individual plants in ten 1 m rows selected at random in weed-free plots only. A series of destructive samples (usually five per season) were taken throughout the growing seasons from 0.5 m² areas within each of the plots. Crop and weed were separated and leaf areas were measured using the leaf area metre. The samples were then dried at 80 °C for 24 h and dry weights determined. Yields and components of yield were assessed at maturity by hand harvesting 2 m² areas. The samples were threshed and the wheat grain was cleaned and dried. Yields were expressed at 85% dry matter.

Assessing dynamics of weed populations and competitiveness

We assessed the impact of local environment and weather on *A. myosuroides* populations by calculating parameter λ which is a ratio of sizes of the weed seed bank at the end and beginning of the growing season (after crop harvest). The number of seed germinating is given by

$$g(ns_0) = g_r \times ns_0 \times \frac{d}{d_{\max}},$$

where g_r is a germination rate, ns_0 is an initial seed number, d is the maximal depth at which seeds germinate and d_{\max} is the depth of the seed bank (25 cm). With a constant herbicide efficiency h , the number of plant p growing in the weed cohort is

$$p(ns_0) = g(ns_0) \times h.$$

The number of seeds produced pr by this cohort is calculated by running Sirius 2010 for a given farming practice, a geographical location, soil characteristics and a yearly set of weather variables:

$$pr(ns_0) = \text{Sirius}(p(ns_0)).$$

Part of this seed production l is lost due to predation or dispersal according to the loss rate l_r :

$$l(ns_0) = pr(ns_0) \times l_r.$$

At the end of the year, a number of old seeds de in the seed bank will die according to the seed persistence sp_r (year):

$$de(ns_0) = \frac{(ns_0 - g(ns_0))}{sp_r}.$$

So the number of seeds ns_1 for a given weed at the end of the year is

$$ns_1 = ns_0 + pr(ns_0) - l(ns_0) - de(ns_0),$$

and the change in the local population size λ can be calculated as follows:

$$\lambda(g_r, h, l_r) = \frac{ns_1}{ns_0}$$

The computation of λ depends on several stochastic factors. The interactions between seed dormancy characteristics, weather and the local soil conditions that drive the proportion of the seed bank that germinates are complex and difficult to predict. Therefore, we modelled the germination rate as a stochastic variable with a distribution derived from experimental data (Fig. S1, Supporting Information). Second, the number of fresh seeds lost is affected by numerous random factors such as predation, weather or harvest method and was also modelled as a stochastic variable following a Gaussian distribution. Finally, to assess the effect of climatic variability, λ must be calculated over many years of daily site-specific weather.

To estimate the change in weed populations, we computed Λ as an average of $\log(\lambda)$ by sampling N times from distributions for germination and seed loss rates as well as weather for the growing season:

$$\Lambda = \frac{\sum_{i < N} \log(\lambda_i)}{N}.$$

The size of the seed bank after y years can be asymptotically estimated as

$$ns_y = ns_0 \times e^{\Lambda y}.$$

Local-scale climate scenarios

Local-scale climate scenarios were based on the output from the HadCM3 global climate model from the multimodel ensemble of global climate models created by the Coupled Model Intercomparison Project (phase 3, CMIP3) (Meehl *et al.*, 2007), which was used in the IPCC 4th Assessment Report (Solomon *et al.*, 2007).

However, the direct use of climate predictions from GCM in conjunction with a process-based impact model, such as Sirius, is not possible. The coarse spatial resolution of GCM of 200–300 km results in significant errors and large uncertainty in their output at a local scale, particularly for precipitation (Knutti *et al.*, 2010). Various downscaling techniques have been developed to underpin studies on regional and local-scale impact assessments, including dynamic downscaling by regional climate models (Jacob *et al.*, 2007), statistical downscaling (Wilby *et al.*, 1998) and WGs (Wilks, 1992; Semenov & Barrow, 1997). In the present study, we used the methodology based on the LARS-WG (Semenov & Stratonovitch, 2010; Semenov *et al.*, 2010).

A stochastic WG is a model which, after calibration of site parameters with observed weather data for that site, is capable of simulating synthetic time-series of daily weather that are

statistically similar to observed weather (Richardson, 1981; Wilks & Wilby, 1999). By altering the baseline site parameters using changes in climate predicted by GCM, it is possible to generate synthetic daily weather for the future. The use of WG in climate change studies allows exploration of the effect of changes in mean climate as well as changes in climatic variability and extreme events (Porter & Semenov, 2005; Semenov, 2007). For our study, we selected climate projections from HadCM3, the global climate model developed at the Hadley Centre of the UK Met. Office for the A1B emission scenario (Nakicenovic & Swart, 2000) and the time periods 1960–1990 (baseline) 2046–2065 (2055A1B) and 2080–2099 (2090A1B) (Pope *et al.*, 2000). Hundred years of daily weather were generated for 18 sites in the United Kingdom (Table S2, Supporting Information) for each climate scenario, baseline, 2055A1B and 2090A1B.

Simulation setup

We configured the soil parameters for the 18 UK locations according to LandIS data (<http://www.landis.org.uk>). We prepared, using LARS-WG, 100 years of site-specific daily weather for each of the three climate scenarios studied. To compute Λ index for a given location and weather scenario, we generated $N = 1500$ yearly simulations by using the 100 years of weather repeatedly and sampling germination rate from the empirical distribution (Fig. S1, Supporting Information) and sampling rates of losses of fresh seed from a normal distribution of mean 0.4 and standard deviation 0.1. A constant herbicide efficiency was used $h = 0.95$.

Results

The current distribution of *A. myosuroides* is the product of the interaction between land use, soil properties and climate (Fig. 1). The majority of establishment is in the autumn as opposed to the spring and the weed is, therefore, largely associated with areas of winter cereals which are concentrated in the south and east of the United Kingdom. However, there also appears to be a climatic constraint to the northward spread of the weed. The predictions of the effects of weather on the distribution and impact of *A. myosuroides* in winter wheat were based on environmental variables from 18 sites in the United Kingdom and the maps of Λ , yield and yield loss were generated by interpolating between these points (Fig. 2). The Northern and Western limit of the weed was accurately described in the model using baseline conditions (Fig. 2a); phenological parameters including thermal time required to reach maturity were identified as being the variables currently limiting the northwards spread of the weed (Fig. 3). The baseline model also accurately reflected current UK yields of winter wheat (the national average was 7.9 t ha^{-1} in 2009, <http://www.fao.org>) under weed-free conditions (Fig. 2d) and the expected yield loss from *A. myosuroides*

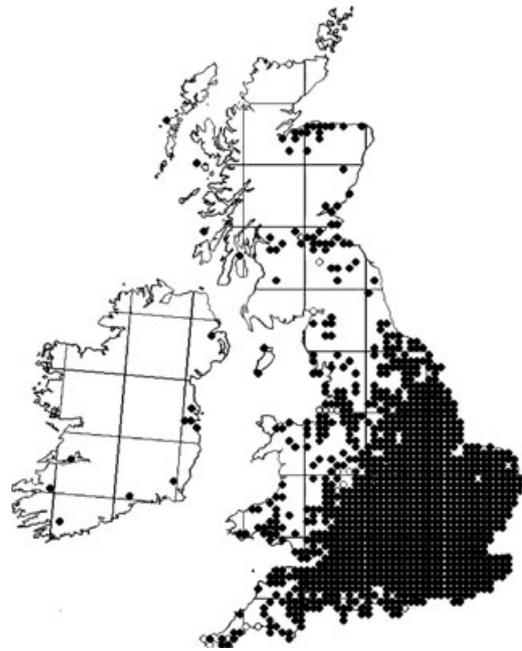


Fig. 1 UK distribution of *Alopecurus myosuroides* Huds. from a series of national vegetation surveys at the hectad scale (after Preston *et al.*, 2002).

ides (Fig. 2g) which is of the order of $0.4\% \text{ plant m}^{-2}$ (Storkey *et al.*, 2003). Finer scale variation under baseline conditions was related to soil type with higher values for Λ and yield loss in the southeast where soils have a higher clay content and reduced drought stress (Fig. S2, Supporting Information). The model performed well when validated against independent datasets of weed productivity and eco-physiological traits measured across a range of environments (Figs S3 and S4, Supporting Information).

The regional effect of soils on the national distribution of *A. myosuroides* became more pronounced under the scenarios for climate change, particularly the 2055A1B simulation (Fig. 2b). The effect of the increased frequency and severity of summer droughts was predicted to be greater on soils with a lower water retention capacity (Fig. 4a). There was also an indication that the higher average temperatures in northern England and Scotland may facilitate the spread of *A. myosuroides* northwards in the United Kingdom. As well as a general increase in the productivity and fitness of *A. myosuroides* populations, increased temperatures and CO_2 resulted in higher national wheat yields in weed-free scenarios (Fig. 2d–f).

There was a more consistent regional effect of climate change on the damage niche of the weed defined by the percentage yield loss (Fig. 3g–i). Under the two climate change scenarios, but particularly 2090A1B, the

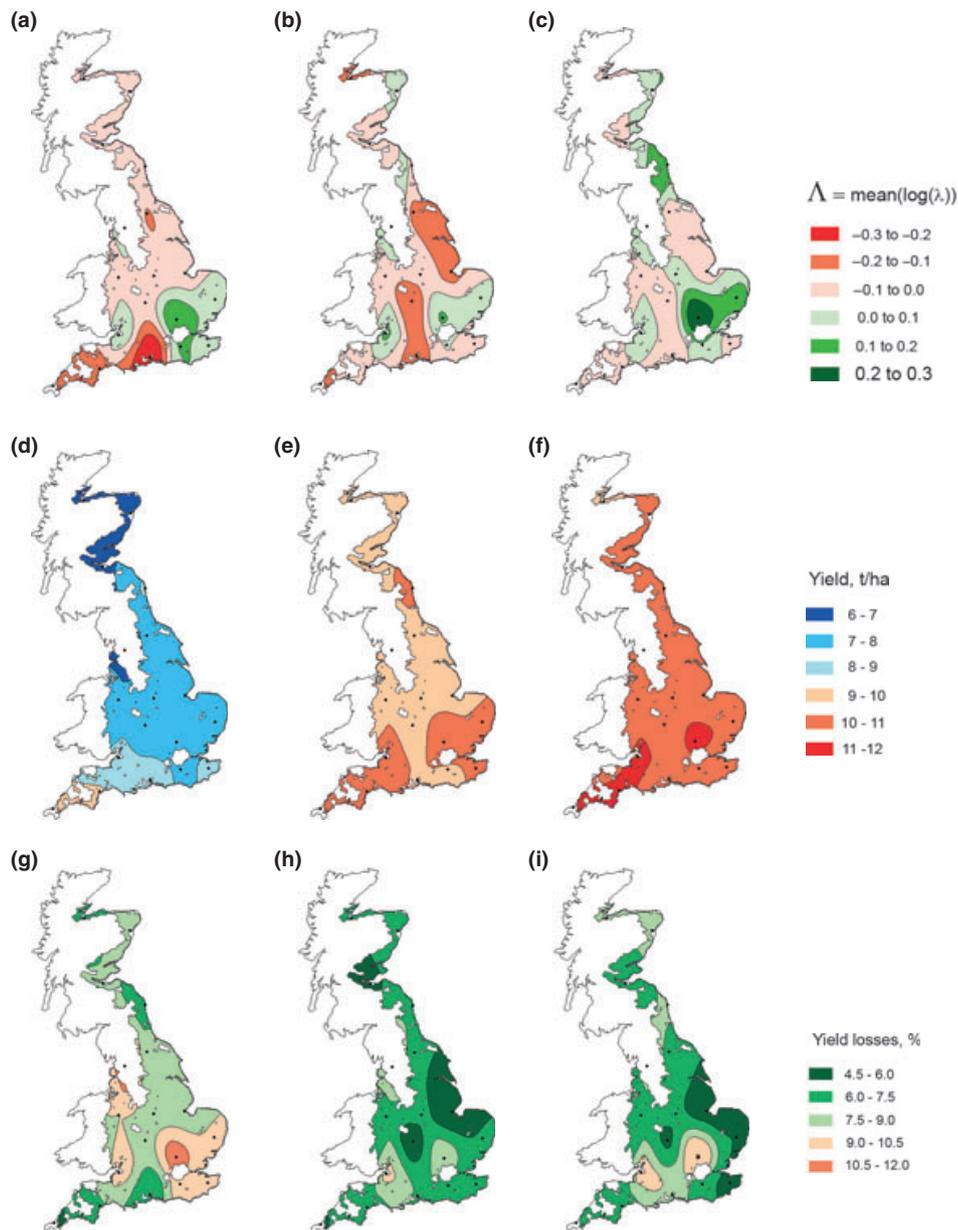


Fig. 2 Output of Sirius 2010 for 18 sites interpolated across the United Kingdom for population change of *Alopecurus myosuroides* (λ) using weather data generated under (a) baseline, (b) 2046–2065 and (c) 2080–2099 conditions, wheat yield under weed-free conditions for (d) baseline, (e) 2046–2065 and (f) 2080–2099 weather and percentage yield loss from weed competition or the ‘damage niche’ using (g) baseline, (h) 2046–2065 and (i) 2080–2099 weather.

competitive balance between the crop and the weed was predicted to shift in favour of the crop. As a consequence, percentage yield loss from *A. myosuroides* was predicted to decrease in the future. The changing dynamics of the interaction between the two species was a product of differential response to climate change. **Both species are C_3 species belonging to the Poaceae** and area therefore similar in terms of their photosynthetic response to increased temperature and CO_2 . However, there are subtle differences in interaction

of development and moisture stress. While both species are predicted to germinate earlier under climate change as a result of increased temperature, this effect is predicted to be marginally greater for the crop (Fig. 3). As a result, the crop gains a competitive advantage early in the season. *Alopecurus myosuroides* is shallower rooting than the crop and this is captured in the model by contrasting functions for root function (Fig. 4b). As a consequence, *A. myosuroides* generally has a higher drought stress index, although the magnitude of this

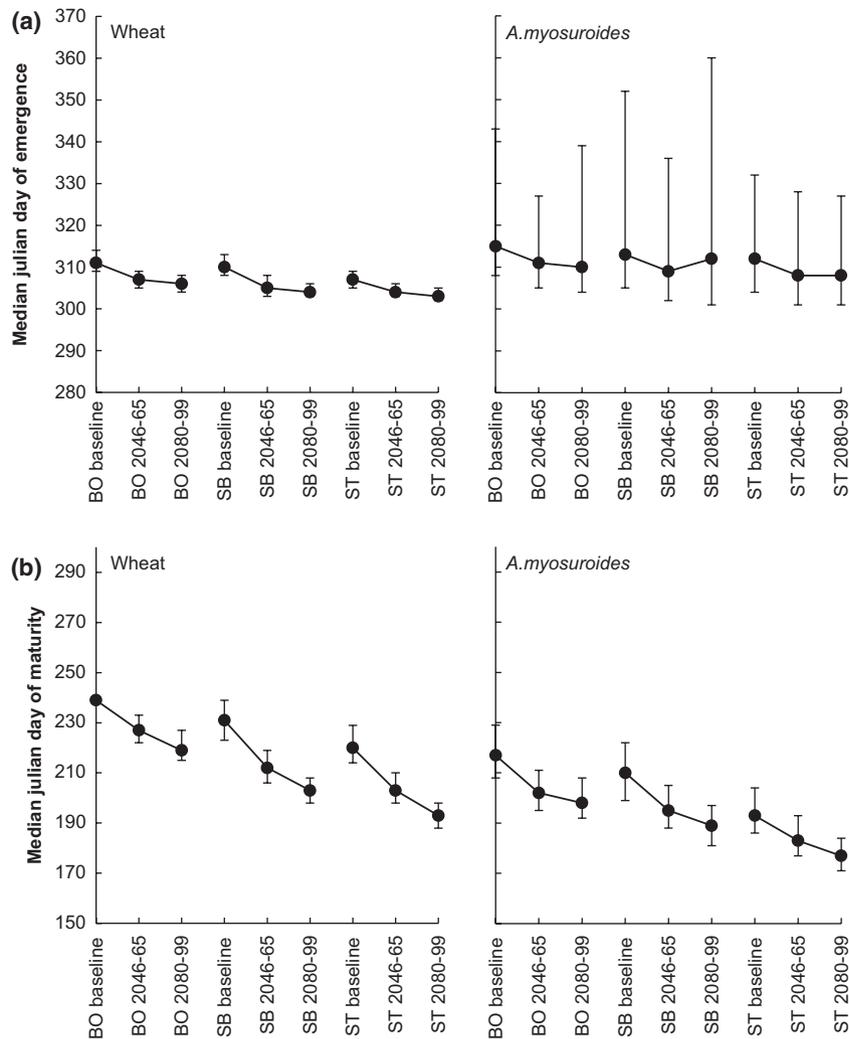


Fig. 3 Impact of climate change on the phenology of wheat and *Alopecurus myosuroides* for three selected sites representing the north–south climatic gradient in the United Kingdom: BO, Boulmer (1°36'W 55°25'N), SB, Sutton Bonington (1°13'W 52°49'N) and ST, Starcross (3°27'W 50°37'N). The median julian day of germination and maturity for each site and time period is plotted with bars representing the 95% percentile derived from the 1500 yearly simulations for each period.

effect is dependent on soil type (Fig. 4a). Because, the weed matures earlier than the crop (Fig. 3), the increasing probability of late season moisture stress is not reflected in an increase in the drought stress index for the weed in the same way as the crop. However, the difference in rooting profiles of the species appears to shift the competitive balance in favour of the crop under scenarios with more frequent periods of moisture stress.

Discussion

The ability of the model to accurately describe the current distribution of *A. myosuroides* under baseline conditions, including the clear Northern limit for the species,

demonstrates the potential of the process-based approach to predict the response of populations to changes in land use, local soil conditions and climate. As opposed to the correlative approach of habitat models, the eco-physiological model allowed the complex interactions of changes in physiological constraints and crop/weed competition in the context of spatially heterogeneous soil properties under climate change to be quantified. As well as predicting shifts in distribution, therefore, our approach facilitates the prediction of changes in the impact of the weed in terms of weed productivity and crop yield loss (previously termed the 'damage niche') to be quantified, with appropriate measures of uncertainty, on a regional scale. **In the case of *A. myosuroides*, a temperate C₃ species,** its potential

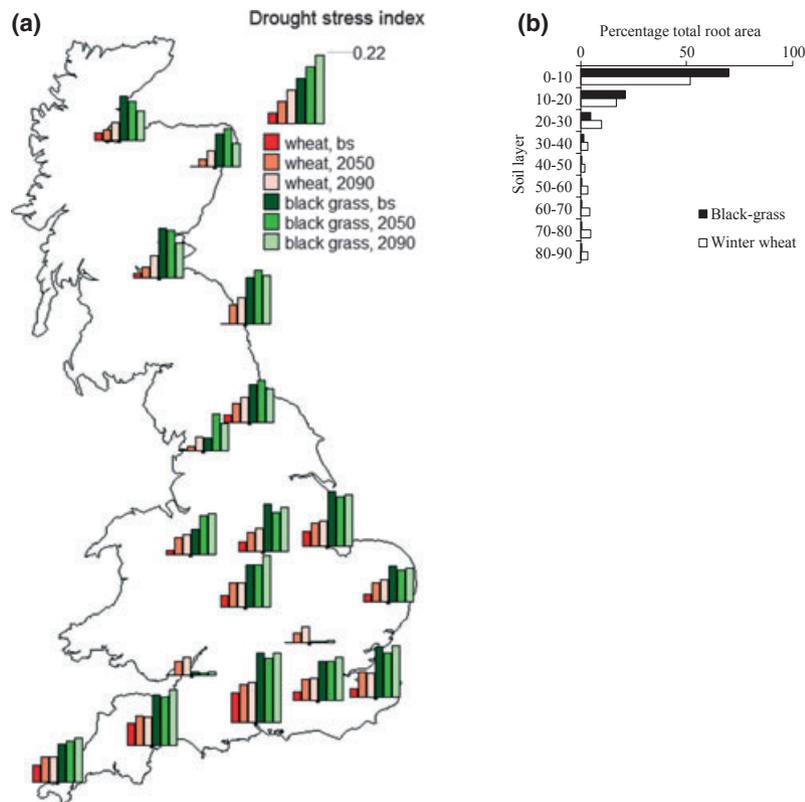


Fig. 4 (a) The drought stress index calculated for wheat and *Alopecurus myosuroides* competing for below ground resources under three climate scenarios. (b) Observed differences in the rooting profiles of wheat and *A. myosuroides* sampled over 2 years in the field at Rothamsted Research, UK (unpublished data).

impact as an agricultural weed was predicted to lessen in response to more frequent and severe water stress events although it may become more of a problem in Scotland. It is likely that contrasting species, for example C_4 weeds which are common in Central or Southern Europe, such as *Ambrosia artemisiifolia*, will respond differently (Essl *et al.*, 2009). A future application of the model developed in this study will, therefore, be the prediction of the probability of the establishment of potentially invasive species as agricultural weeds under climate change.

In the scenarios used in this study, no attempt was made to account for changes in agronomy in response to climate such as earlier drilling dates or a change in cropping patterns or herbicide use. However, in real systems weather and crop management are intricately linked with the timing of operations, for example drilling date, determined by local weather and characteristics of the preceding crop. A change in cropping, for example an increase in the proportion of spring crops sown, would be expected to affect the damage niche of a weed to a similar or larger degree as changes in the climate. While the objective of this study was to isolate the potential impact of climate on weeds, the process-

based approach also has the capacity to integrate data on the likely effect of climate change on management practices in the future.

The disadvantage of using a process-based approach to modelling plant dynamics as opposed to correlative habitat models is that the large number of eco-physiological parameters require calibration for each species. For a small number of weeds with a high economic importance, empirical data are available in the weed science literature to calibrate and validate the model (Deen *et al.*, 2003). However, alternative approaches will need to be developed to extend the approach to the wider weed community. One option is to develop screening protocols for key model parameters, for example the base temperature of germination (Steinmaus *et al.*, 2000). Alternatively, it may be possible to estimate model parameters from data on plant traits available in ecological databases (Gardarin *et al.*, 2010b); for example seed mass can be related to a number of parameters determining germination and fecundity (Gardarin *et al.*, 2010a). An extension of this approach would be to identify weed functional groups or ideotypes with similar suites of functional traits and responses to environmental change. Modelling the

weed flora at the level of this level would facilitate the prediction of more general functional shifts in weed infestations, for example a shift from C₃ to C₄ species if drought becomes a more dominant environmental driver.

Finally a major challenge to any attempt to model the impact of climate change on the damage niche of an agricultural weed, regardless of whether it takes a correlative or mechanistic approach, is the capacity of weeds to adapt (Clements & Ditommaso, 2011). Failing to account for the propensity of weeds with high fecundity and short duration of population cycling to adapt to new conditions, both through phenotypic plasticity and genotypic adaptation, will lead to an under-estimate possible shifts in distribution and impact. The incorporation data on intra-specific variability within weed species (particularly at the leading edge of its distribution) will, therefore, need to be an important component of the future development of models of the type used in this study.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Location and site characteristics of experiments used to validate process-based model of *Alopecurus myosuroides* growth and competition.

Table S2. Location and site characteristics the 18 locations used in the climate change impact simulations.

Table S3. Soil description for the sites in Table S2.

Figure S1. Probability distribution of germination from a seed bank of known size observed on 54 plots at five sites over 3 years (Table S1) as part of the validation experiments.

Figure S2. Available water capacity (mm) for 18 sites used in model.

Figure S3. Example of output from Sirius 2010 against observed data from validation experiments.

Figure S4. Example of output from Sirius 2010 against observed data from validation experiments.

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