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MODELLING THE POPULATION DYNAMICS OF AN ARABLE WEED AND ITS EFFECTS UPON CROP YIELD

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SUMMARY

(1) A model is developed for spring wheat infested by various densities of an annual weed, *Agrostemma githago* L. Data on the survival and reproductive performance of the crop and the weed, obtained in experimental monocultures and mixtures, are then used to calculate the expected yields of crop and weed for any combination of initial densities.

(2) The model is used to predict the changes in the density of *Agrostemma* from season to season. In the absence of control, and starting with a density of one *Agrostemma* plant ha^{-1}, the weed infestation would be expected to cause appreciable yield loss to spring wheat after 6 years.

(3) Partial control of the weed, by removal of seeds and seedlings, is predicted to have little effect upon the weed density. More than 50% of seeds must be removed annually in order to reduce appreciably the rate of increase of weed density and the density at equilibrium; over 90% control is required to eradicate *Agrostemma.* These findings help to explain the recent decline of *Agrostemma* in British cereal crops.

(4) The model can be easily adapted for other weed species, as long as age structure does not vary. The development of cost-effective strategies for weed control will probably depend on the use of models such as this one which can estimate the effects of available control options upon the behaviour of weed populations and thence upon crop yields.

INTRODUCTION

The use of herbicides has not eliminated weed problems in agriculture. Indeed, changes in the weed flora (Chancellor 1977) and the appearance of resistance to herbicides (LeBaron & Gressel 1982) have brought about additional problems, often increasing costs to the producer. There is an increasing need for improved strategies in weed control. An important element of such management strategies is the development of population models that are capable of predicting the results of control measures on weed densities and hence on crop yields (Mortimer & Firbank 1983).

The birth and death rates of plants are influenced by two sets of factors: (i) density-independent factors such as climate, soil type and cultural practices, and (ii) density-dependent factors which arise when the available resources are limited and must be shared among the number of plants present. The effects of density-independent factors may be estimated by using simple probability estimates of emergence (e.g. Naylor 1970), survival and reproduction (e.g. Sagar & Mortimer 1976). More complex models are needed to describe the effects of density dependence (e.g. Watkinson 1980). These two sets of factors may interact (e.g. Watkinson 1982), and both should be addressed by predictive models of weed populations.

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The model presented in this paper relates the size of a weed population in one generation to its size in the previous generation, taking density-dependent and density-independent factors into account. The model also describes the expected effect of the weed on crop yield. It is used to describe the population dynamics of the corncockle *Agrostemma githago* L. in a crop of spring wheat *Triticum aestivum* L., as affected by different levels of weed control. Whilst *Agrostemma* is no longer an economically important weed in Great Britain, aspects of its life cycle make it particularly suitable for demonstrating this modelling technique. Furthermore, the results of the model may be compared with the known history of this species, and its response to control in the past.

Agrostemma *as a weed*

The life cycle of *Agrostemma* resembles that of many other winter annuals native to the eastern Mediterranean region. The seeds have only a short after-ripening period and no chilling requirement, and can therefore germinate at any time of year given sufficient moisture. Ungerminated seeds do not persist in the soil. Autumn-germinated seeds overwinter to flower and set seed in the following summer; plants that emerge in spring behave as summer annuals (Svensson & Wigren 1983; Firbank 1984).

Agrostemma was regarded as a pernicious weed because it caused a depression in crop yield and the seeds were a poisonous impurity in flour (Henslow 1901). It has long been a weed of cereal crops (Thompson 1973), largely because the seeds could not all be separated from the cereal grain because of their similarity in size (Anon. 1910). Selection favoured the precise matching of *Agrostemma* seed size to the grain size and the retention of seeds in their capsules to be harvested and resown along with the grain. By acting as a crop mimic, thereby satisfying its requirement for predictably open habitats, *Agrostemma* was able to colonize Europe and beyond (Thompson 1973; Firbank 1984). It failed to establish in hedgerows and any seeds not harvested were not dispersed widely enough to reach newly disturbed sites. In order to persist, it relied upon continuous reintroductions from contaminated grain, and the introduction of improved seed-cleaning techniques during the early 20th century inevitably caused *Agrostemma* to decline (Thompson 1973; Firbank 1984). It virtually ceased to be recorded as an impurity of British cereal grain during the 1950s (Broad 1952; Tonkin 1968; R. Flood pers. comm.).

EXPERIMENTAL METHODS

The data for the model were obtained from experiments in which *Agrostemma githago* and *Triticum aestivum* cv. Sicco were sown on rotovated land at the University of East Anglia, Norwich. The two species were sown in monocultures and 1:1 mixtures at five overall densities (16, 40, 120, 400 and 1200 plants m^{-2}). The seeds were sown at random within each of three replicate plots ($0{\cdot}25$ m^2) for each treatment between 8 and 11 May 1981. The number of established seedlings was counted on 29 May 1981. Seedlings from spare plots were then transplanted to the experimental plots to restore the densities to the original levels. All shoots were harvested during 11–29 August 1981 and subsequently dry weighed. Further details of this experiment are given by Firbank & Watkinson (1985).

The relationship between seed production and shoot dry weight was ascertained in a separate experiment in which seeds of *Agrostemma* were sown among *Triticum aestivum* cv. Sicco in two plots of 1 m^2 at each of three densities (8, 64 and 512 seeds m^{-2}) on 28 April 1980. The wheat was sown at a density of 512 seeds m^{-2}. The plants were harvested on 28 August 1980, and the number of seeds per plant and the shoot dry weights of sampled plants were recorded.

A MODEL OF THE DYNAMICS OF A WEED–CROP SYSTEM

Competition between a weed and a crop

The density of established seedlings, N_i, is dependent upon the sowing density, N_s, and the proportion of the seeds sown which establish, q. Thus:

$$N_i = q\, N_s. \tag{1}$$

Density-dependent mortality in a monoculture, as a result of self-thinning, is described by the equation,

$$N = N_i\,(1 + m\, N_i)^{-1}, \tag{2}$$

where N is the density at harvest and m^{-1} is the asymptotic density of harvest after self-thinning from very high seedling densities (Yoda *et al.* 1963). In a mixture, the survival and yield of each species are affected by the densities of both species, though not necessarily to the same extent. Hence,

$$N_A = N_{iA}\,(1 + m_A\,(N_{iA} + \gamma\, N_{iW}))^{-1}, \tag{3}$$

and

$$N_W = N_{iW}\,(1 + m_W\,(N_{iW} + \delta\, N_{iA}))^{-1}, \tag{4}$$

where A and W refer to *Agrostemma* and wheat respectively, and γ and δ are the competition coefficients representing the impact of plants of one species on the survival of plants of the other (Lonsdale 1981).

The mean shoot dry weight per plant, w, can be expressed by the equation,

$$w = w_m\,(1 + aN)^{-b}, \tag{5}$$

where w_m is the mean shoot dry weight of isolated plants growing in that environment and a and b are parameters (Watkinson 1980). In mixture,

$$w_A = w_{mA}\,(1 + a_A\,(N_A + \alpha N_W))^{-b_A}, \tag{6}$$

$$w_W = w_{mW}\,(1 + a_W\,(N_W + \beta N_A))^{-b_B}, \tag{7}$$

where α and β are competition coefficients describing the equivalences between the two species (Watkinson 1981). All four competition coefficients, α, β, γ and δ, may be strongly influenced by the relative emergence times of the two species (Firbank & Watkinson 1985). Equations (2)–(7) apply only if the plants are dispersed approximately at random and are fitted to log-transformed data using iterative least-squares minimization.

Seed production by a plant, s, is often an allometric function of the shoot dry weight:

$$s = c\, w^k, \tag{8}$$

where c and k are population-specific parameters which do not appear to be influenced by the presence of a second species (Watkinson 1981). The use of eqns (2)–(8) is described by Firbank & Watkinson (1985).

Competition between Agrostemma *and wheat*

The proportion of seeds of each species that emerged was not significantly affected by density or by the presence of the other species ($P > 0{\cdot}05$). The overall emergence rates q were 0·64 for *Agrostemma* and 0·49 for wheat. Hence, from the sowing densities of N_{sA} and N_{sW} it is possible to calculate the seedling densities of *Agrostemma*, N_{iA}, and wheat, N_{iW}, from

$$N_{iA} = q_A N_{sA} = 0{\cdot}64\, N_{sA}, \tag{9}$$

$$N_{iW} = q_W N_{sW} = 0{\cdot}49\, N_{sW}. \tag{10}$$

The relationships between the density of plants at maturity and the density of seedlings for each species (see eqns 3 and 4) were described by the equations:

$$N_A = N_{iA}\,(1 + 4{\cdot}2 \times 10^{-4}\,(N_{iA} + 0{\cdot}62\, N_{iW}))^{-1}, \quad r^2 = 0{\cdot}93, n = 30, \tag{11}$$

$$N_W = N_{iW}\,(1 + 6{\cdot}4 \times 10^{-4}\,(N_{iW} - 0{\cdot}42\, N_{iA}))^{-1}, \quad r^2 = 0{\cdot}99, n = 30, \tag{12}$$

indicating that $m_A = 4{\cdot}2 \times 10^{-4}$ m^2, $m_W = 6{\cdot}4 \times 10^{-4}$ m^2, $\gamma = 0{\cdot}62$ and $\delta = -0{\cdot}42$. The fact that δ is negative ($P < 0{\cdot}001$) may imply that the *Agrostemma* seedlings protected the wheat seedlings from weather, pests or pathogens. The relationships between mean shoot dry weight per plant and density (see eqns 5 and 6) were described by the equations:

$$w_A = 31{\cdot}7\,(1 + 0{\cdot}063\,(N_A + 0{\cdot}41\, N_W))^{-0{\cdot}72}, \quad r^2 = 0{\cdot}94, n = 29, \tag{13}$$

$$w_W = 46{\cdot}8\,(1 + 0{\cdot}24\,(N_W + 1{\cdot}63\, N_A))^{-0{\cdot}67}, \quad r^2 = 0{\cdot}91, n = 30, \tag{14}$$

indicating that $w_{mA} = 31{\cdot}7$ g, $w_{mW} = 46{\cdot}8$ g, $a_A = 0{\cdot}063$ m^2, $a_W = 0{\cdot}24$ m^2, $\alpha = 0{\cdot}41$, $\beta = 1{\cdot}63$, $b_A = 0{\cdot}72$ and $b_W = 0{\cdot}67$. The allometric relationship between the number of seeds produced per plant and shoot dry weight (eqn 8) was estimated for *Agrostemma* to be:

$$s_A = 30{\cdot}7\, w_A^{\,1{\cdot}03}, \quad r^2 = 0{\cdot}92, n = 94, \tag{15}$$

and for wheat to be:

$$s_W = 11{\cdot}4\, w_W^{\,0{\cdot}96}, \quad r^2 = 0{\cdot}93, n = 41. \tag{16}$$

These relationships are shown in Fig. 1, the estimated errors of the parameters are given in Table 2 and r^2 values refer to log-transformed data.

The combination of eqns (9), (11), (13) and (15), and of (10), (12), (14) and (16) allows the seed output from plants of each species to be related to the initial sowing densities of both so that the seed production per unit area can be estimated (Fig. 2). In both species, the higher the initial density of that species the greater the seed production in both monoculture and mixtures. The loss in yield as a result of the presence of a second species depends upon the densities of the two species. Thus the seed production of wheat at low densities is reduced by a factor of ten by a high density of *Agrostemma*, but the effect is much smaller at high wheat densities. Similarly, the seed output of *Agrostemma* is considerably affected by the presence of the crop at low *Agrostemma* densities, but not at high densities.

Forecasting the long-term behaviour of a weed population

Weed-control strategies require consideration of longer-term implications. Although yield losses in the current year may be acceptable, any resulting increase in the future level of infestation may give rise to unacceptable losses. An understanding of the long-term

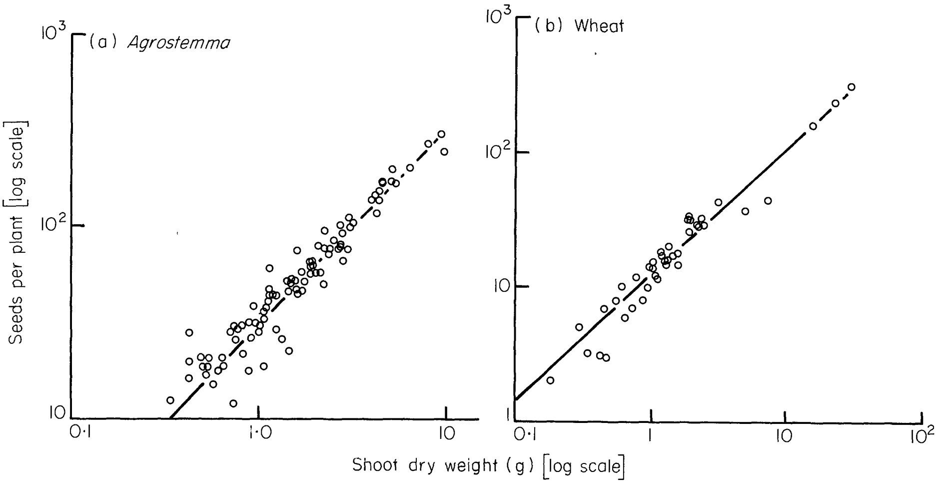

FIG. 1. The allometric relationships between the number of seeds produced per plant, s, and shoot dry weight per plant, w, for (a) *Agrostemma* ($s = 30{\cdot}7\ w^{1{\cdot}03}$) and (b) wheat ($s = 11{\cdot}4\ w^{0{\cdot}96}$).

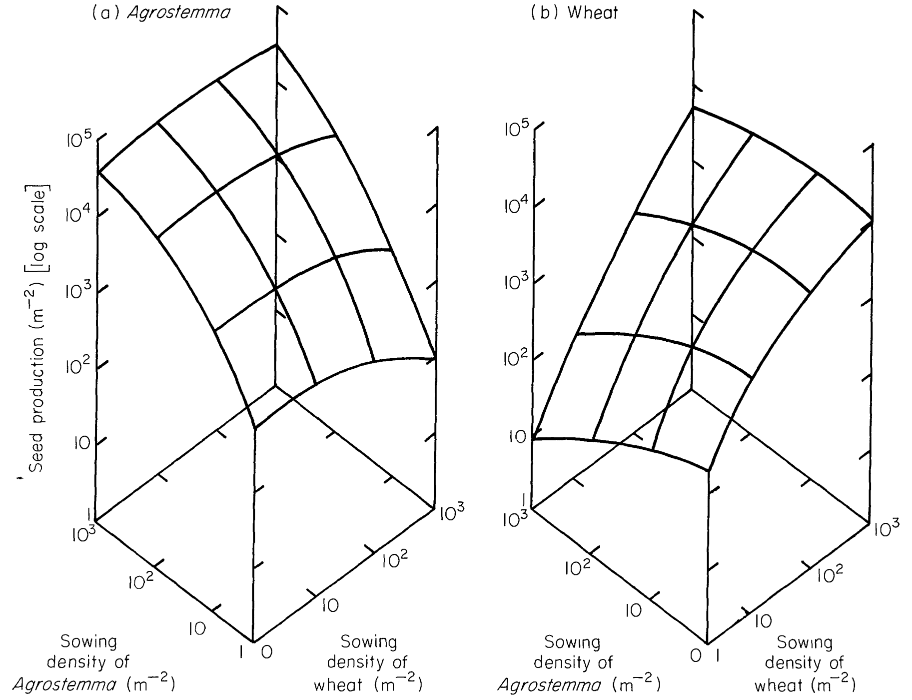

FIG. 2. Relationships between the total number of seeds produced m^{-2} and the sowing densities of both species (m^{-2}) of (a) *Agrostemma* and (b) wheat as estimated using eqns (9)–(16). Note that the horizontal axes are scaled as log (N + 1).

population dynamics of the weed is therefore required if longer-term risks are to be assessed.

The seeds of *Agrostemma* are held within the capsule until the late autumn (Firbank 1984), and therefore they are almost all harvested along with the crop. The harvested grain would thus comprise a mixture of wheat and *Agrostemma* seeds. Any seeds shed during harvest germinate quickly and are easily killed by cultivation or by herbicides. Therefore, as long as clean seed is imported for sowing, the weed is rapidly eliminated.

Agrostemma was a pernicious weed in Great Britain at a time when some of the harvested grain was retained for sowing as the next season's crop. These seeds would have been contaminated by *Agrostemma* in the same proportion as in the total harvest, assuming that only a negligible fraction of the seeds were lost during harvesting. Therefore, the weed–crop model (eqns (9)–(16)) may be applied to estimate the future damage to crop yield under this particular system.

If the sowing rate of wheat is y seeds m^{-2}, and in year i it is contaminated with x_i seeds m^{-2} of *Agrostemma*, then the total harvest can be calculated from eqns (9)–(16) and will be $N_W s_W$ seeds of wheat m^{-2} with $N_A s_A$ seeds of *Agrostemma* as impurities (where N is the number of plants at harvest and s is the mean number of seeds produced per plant). If the wheat is not cleaned, the sown seeds (y wheat seeds m^{-2}) will be contaminated with x_{i+1} seeds m^{-2} of *Agrostemma*, where

$$x_{i+1} = \frac{N_A s_A}{N_W s_W} \cdot y. \tag{17}$$

The population density of *Agrostemma* may be predicted over a series of years using this equation, if the crop–weed system satisfies the assumptions implicit in the model. These assumptions are that (i) the weed and crop are dispersed approximately at random, and (ii) all of the parameters remain approximately constant with time. Seeds of wheat and *Agrostemma* were harvested, stored and sown together, suggesting that the first assumption is reasonable in this case. Furthermore, both species germinate quickly, and so the relative emergence times are constant from year to year, thus minimizing variations of the competition coefficients. The degree of variation to be expected in the other parameters is not known.

On the basis of this model, the density of *Agrostemma* is expected to increase exponentially initially, and eventually to reach an asymptote at a very high density as a result of self-thinning (Fig. 3). This equilibrium density is hardly affected by the density of the crop (Fig. 3). The number of wheat grains harvested, and hence the yield of wheat, is affected by the sowing density of the crop (Fig. 3), but is not greatly affected by the weed density until the latter reaches about 1000 plants m^{-2}. At high weed density, the yield reduction of wheat is greater at low sowing densities.

Modelling the effect of control measures

A variety of control measures have been recommended to eliminate *Agrostemma*; these include the use of clean grain, the hand-pulling of mature plants and howing and harrowing to kill any seedlings (Anon. 1910). The effect of these control methods can be modelled using a single parameter j which describes the losses between seed production and seedling establishment in addition to those that result from natural mortality, accounted for by the parameter q which describes the success of establishment without controls. The effect of

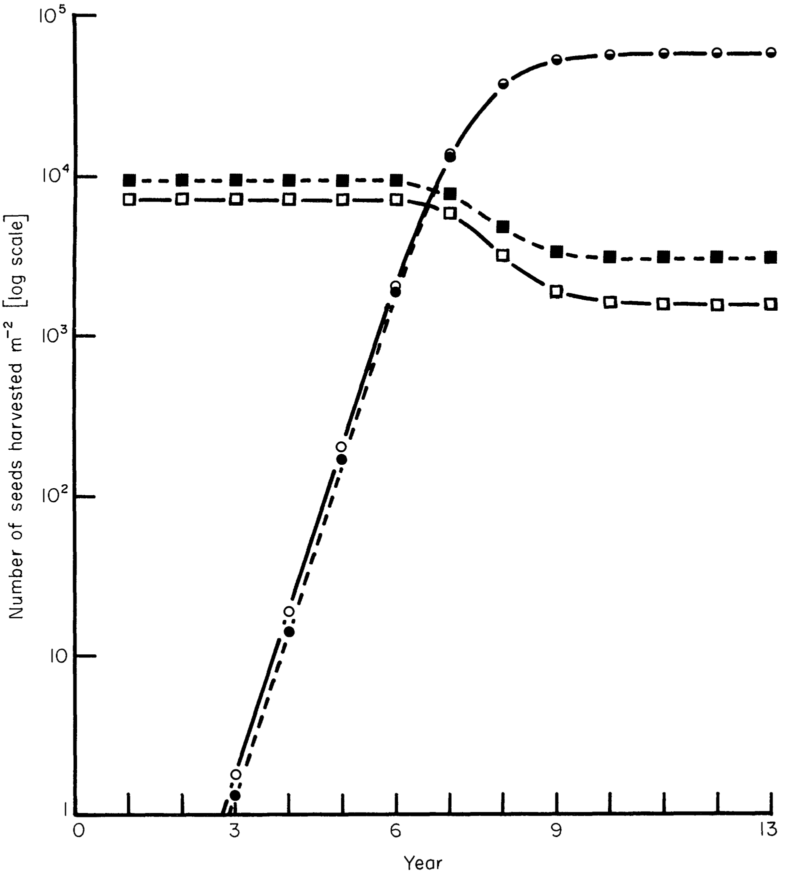

FIG. 3. Seed harvests in successive years following an initial infestation of one seed of *Agrostemma* (○, ●) ha^{-1} amongst wheat sown at 500 seeds m^{-2} (□) and 1000 seeds m^{-2} (■).

these controls may be deduced from the equation

$$x_{i+1} = \frac{N_A s_A}{N_W s_W} . y . (1 - j), \tag{18}$$

where N_A, s_A, N_W and s_W are derived from x_i and y (see Table 1 for the full model).

The asymptotic density of *Agrostemma* is reduced by the control measures, but the effect is very small if the control practice reduces plant and seed numbers by less than 80%. Above this level of control, the equilibrium density falls sharply (Fig. 4), and eradication occurs if control exceeds approximately 90% (Fig. 4). This sharp decline is a result of the interaction between the density-independent control measures and the non-linear response of plant fecundity to density.

The degree of control also determines the time required to reach either the asymptotic density or the elimination of the weed (Fig. 5): the former is increased and the latter decreased by increased levels of control.

The effects of variation of the parameters

In the model given in Table 1, all of the parameters are assumed to be constant from year to year. In practice, some of these parameters are likely to vary with different weather

TABLE 1. A population model of infestations of *Agrostemma githago* in spring wheat. The changing population levels m^{-2} are described for a complete season according to equations given in the text (shoot dry weight is measured in g)

Initial sowing rates m^{-2}:	
Agrostemma	x_i
Wheat	y
No. seedlings emerging m^{-2}:	
Agrostemma	$N_{iA} = 0{\cdot}64 x_i$
Wheat	$N_{iW} = 0{\cdot}49\, y$
No. plants surviving to harvest m^{-2}:	
Agrostemma	$N_A = N_{iA}(1 + 4{\cdot}2 \times 10^{-4}(N_{iA} + 0{\cdot}62N_{iW}))^{-1}$
Wheat	$N_W = N_{iW}(1 + 6{\cdot}4 \times 10^{-4}(N_{iW} - 0{\cdot}42N_{iA}))^{-1}$
where	$N_{iW} > 0{\cdot}42N_{iA}$
otherwise	$N_W = N_{iW}$
Mean shoot dry weight per plant (g):	
Agrostemma	$w_A = 31{\cdot}7(1 + 0{\cdot}063(N_A + 0{\cdot}41N_W))^{-0{\cdot}72}$
Wheat	$w_W = 46{\cdot}8(1 + 0{\cdot}24(N_W + 1{\cdot}63N_A))^{-0{\cdot}66}$
No. seeds produced per plant:	
Agrostemma	$s_A = 30{\cdot}7{w_A}^{1{\cdot}03}$
Wheat	$s_W = 11{\cdot}4{w_W}^{0{\cdot}96}$
Seed production m^{-2}:	
Agrostemma	$N_A s_A$
Wheat	$N_W s_W$
Proportion of seeds surviving cleaning and other controls:	
Agrostemma	$(1 - j)$
No. seeds surviving seed cleaning and other controls m^{-2}:	
Agrostemma	$N_A s_A(1 - j)$
Sowing rates in year $i + 1$ m^{-2}:	
Agrostemma	$x_{i+1} = \dfrac{N_A s_A}{N_W s_W}(1 - j)\, y$
Wheat	y

conditions and management practices. Whilst long-term field studies are required to assess the extent and effects of such variation (Reader 1985), a simple stability analysis of the model can give useful insights into the possible effects of variation within the wheat–*Agrostemma* system.

The effects of variability of each parameter in turn upon the predicted crop yields over 5 years were assessed by running the model, whilst selecting the chosen parameter from a distribution of possible values in each year. This procedure was repeated 100 times for each parameter to give the mean and (more importantly) the standard error of the predicted cumulative yield of the crop. The parameter values were drawn from normal distributions using mean values estimated from the data and firstly the standard errors estimated from the data and secondly nominal standard errors of 0·1 times the mean. Only the competition coefficients α, β, γ and δ were allowed to take negative values. In addition, the model was run with all parameters allowed to vary simultaneously with standard errors of 0·1 times their mean values.

The expected standard error of crop yields summed over 5 years was small when parameters defining the growth of *Agrostemma* were varied (Table 2). The density-dependent regulation of *Agrostemma* populations appears to have been sufficient to dampen variation in crop yield over the medium term. The effects of varying the competition coefficients again appeared to be minor compared with the variation resulting from changes in the parameters describing crop yield and survival. In the example given in Table 2, variation around a mean control efficiency of 0·85 caused substantial variability in yield; had the mean control efficiency been smaller, then the standard error of yield

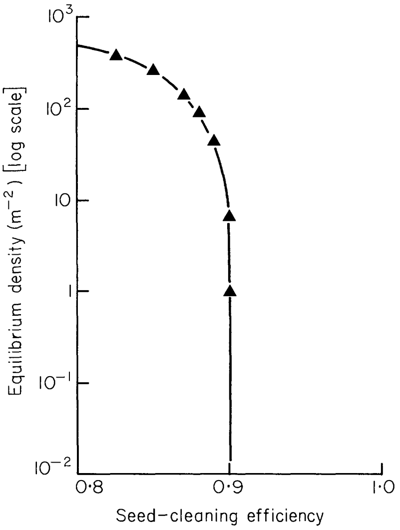

FIG. 4. The effect of different levels of the efficiency of the removal of *Agrostemma* seeds from wheat seed on the density of mature plants of *Agrostemma* at equilibrium amongst wheat sown at 500 seeds m^{-2}.

TABLE 2. The stability of cumulative gross wheat yields over 5 years is assessed with respect to the variation of each parameter of the wheat–*Agrostemma* model (Table 1). The model was used to project crop yields over 5 years with a crop sowing density of 500 seeds m^{-2} initially infested with 10 seeds m^{-2} of *Agrostemma* with an annual seed-cleaning efficiency of 0·85. The runs were replicated 100 times to give the standard error of gross crop yield following the variation of each parameter in turn using a normal distribution of (a) standard error as estimated from the data and (b) a nominal standard error of 0·1 of the mean parameter value. Finally, all parameters were varied simultaneously using the nominal standard errors. Crop yields are given as 10^3 grains m^{-2} (see text for parameter definitions and other details)

		(a) Estimated standard errors			(b) Nominal standard errors	
Parameter	Estimated mean value	Estimated S.E. of parameter	Mean gross crop yield	S.E. of gross crop yield	Mean gross crop yield	S.E. of gross crop yield
q_A	0·64	0·19	37·4	1·02	37·3	0·33
q_W	0·49	0·18	35·9	3·74	37·2	0·79
m_A	$4{\cdot}2 \times 10^{-4}$	$5{\cdot}7 \times 10^{-4}$	37·5	0·17	37·3	0·09
m_W	$6{\cdot}4 \times 10^{-4}$	$6{\cdot}4 \times 10^{-4}$	36·5	1·05	37·3	0·10
γ	0·62	0·75	37·3	0·19	37·3	0·09
δ	−0·42	0·16	37·3	0·08	37·3	0·09
w_{mA}	31·7	12·5	37·3	1·17	37·3	0·26
w_{mW}	46·8	23·4	35·4	8·55	37·0	1·65
a_A	0·063	0·37	39·1	0·45	37·2	0·15
a_W	0·24	0·24	44·8	18·94	37·5	1·10
b_A	0·72	0·066	37·3	0·38	37·3	0·42
b_W	0·67	0·040	37·9	3·27	38·2	5·15
α	0·41	0·18	36·7	1·16	37·3	0·15
β	1·63	0·42	37·3	0·29	37·3	0·08
c_A	30·7	1·53	37·3	0·13	37·3	0·27
c_W	11·4	0·83	37·4	1·35	37·5	1·99
k_A	1·03	0·052	37·3	0·29	37·2	0·62
k_W	0·96	0·065	37·6	1·36	37·6	2·22
j	0·85	0	37·3	0	36·4	2·37
			All parameters varying:		38·6	7·35

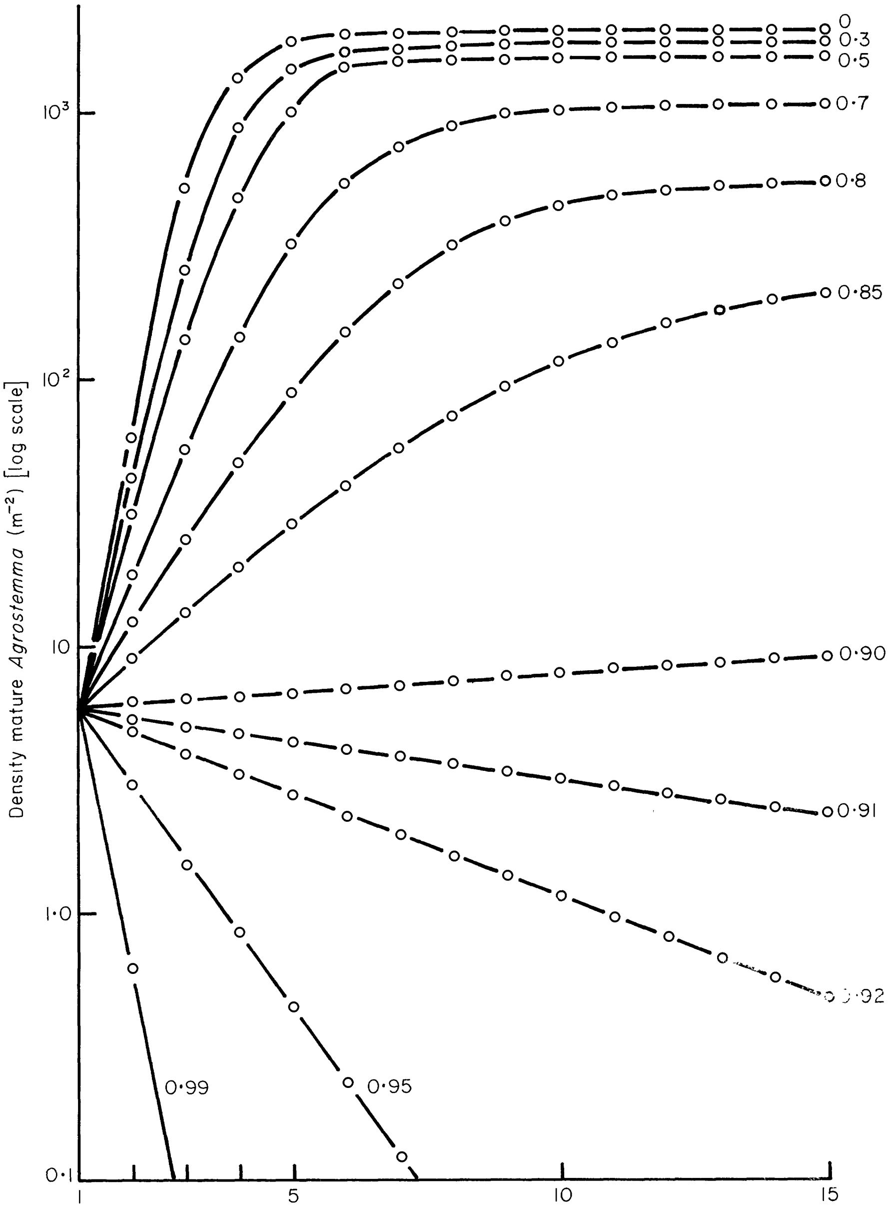

FIG. 5. The effect through time of different levels of the efficiency of the removal of *Agrostemma* seeds from wheat seed (0–0·99) on the density of *Agrostemma* following an initial infestation of ten seeds of *Agrostemma* m^{-2} amongst wheat sown at 500 seeds m^{-2}.

would have been reduced (from consideration of Fig. 5). Not surprisingly, the simultaneous variation of all parameters gave rise to a high standard error for the predicted crop yields—greater than would be expected if the likely correlations between parameters were fully understood and accounted for.

DISCUSSION

The behaviour of *Agrostemma* as a weed is relatively easy to model because of the life cycle of the weed and its synchrony with that of the crop. The same modelling approach can be applied to other weed species, after appropriate modification depending on the life cycle of the weed and the effects of possible control measures. For example, the model could be readily applied to sterile brome (*Bromus sterilis* L.), which, like *Agrostemma*, has discrete, even-aged generations (Firbank *et al.* 1984). However, a more sophisticated model is needed for *Bromus* because of the greater variety of possible fates of the seeds. Far fewer seeds are harvested with the crop than with *Agrostemma*; the rest may be burned or removed with the straw, ploughed in or the seedlings killed using herbicides. The survival of seeds differs between some of these practices (Froud-Williams 1983) and between years (Firbank, Mortimer & Putwain 1985). Seedling survival may even be density-dependent in *Bromus* (Firbank, Mortimer & Putwain 1985). In the case of those weeds (e.g. *Avena fatua* L.) which have a wide range of emergence times within the crop, modelling would require explicit consideration of age structure of the population (Mortimer 1983) because plants of different ages have different competitive effects. As a result of the variation of age structure, the yield of wheat infested by *Avena* is not closely correlated with weed density and the rate of increase of the density of *Avena* is highly variable (Firbank *et al.* 1984). The dynamics of many weed species are further complicated by the dormancy of propagules. Models of the dynamics of seed banks have been developed by Charlesworth (1980), MacDonald & Watkinson (1982) and Mortimer (1983). No models have yet been developed which incorporate all these various components in conjunction with density dependence.

Population models are of value for efficient weed management by predicting population changes and also by identifying aspects of the population biology which are critical to efficient control. Weed management methods may therefore be targeted to susceptible points in the life cycle. The findings of the model presented in this paper suggest that the critical aspect of the control of *Agrostemma* was the need to separate *Agrostemma* seed from the grain with the utmost efficiency. During the Middle Ages, typical infestations were of around ten seeds per thousand grain (from cesspit finds, P. Murphy pers. comm.), implying that *Agrostemma* was sown at approximately two to five plants m^{-2}. Even allowing for variation of the parameters of the model with cereal variety, growing conditions and the presence of other weeds, a high level of control must have been enforced to maintain this level of infestation (from Figs 4 and 5). The existence of subspecies which mimic specific crops for seed size (Thompson 1973; Hammer, Hanelt & Knupffer 1982) implies that there was selection pressure on seed size resulting from efficient-seed cleaning. Therefore, an increase in seed-cleaning efficiency of even 5% during the 20th century may have been sufficient to cause the rapid decline in *Agrostemma* populations which preceded the widespread use of herbicides (from Fig. 4). The persistence of *Agrostemma* in rye crops in Great Britain until approximately 1960 (Broad 1952; Tonkin 1968; R. Flood pers. comm.) possibly resulted from a closer similarity between weed and crop seed sizes which reduced the efficiency of control.

It is most encouraging that a deterministic model, using data from one year in one experimental site, appears to be representative of the overall situation. In addition, the simple stability analysis suggests that in the medium term, variations in the growth and survival of the weed need not be responsible for unacceptable errors in the predicted crop yields. Accurate descriptions of the parameters of crop yield are essential, however, for successful modelling, as exemplified by the effects of the poor estimates of w_{mW} and a_W—resulting from the lack of data at very low densities (Firbank & Watkinson 1985)—upon the predicted standard error of yield (Table 2).

Weed-control strategies will require the integration of population and economic models (Mortimer 1983; Mortimer & Firbank 1983); population models are needed to forecast accurately weed densities and resulting losses in crop yields, whilst economic models will be needed to analyse the direct costs of control options in relation to the benefits of the likely reductions in losses to yield quantity and quality.

The nature of models which can be used to define control strategies for insect pests has already been recognized (e.g. Conway 1981; Norton, Sutherst & Maywald 1983; Shoemaker 1983). However, the few examples of such models for the control of weeds utilize simplistic models of weed population dynamics (e.g. Doyle *et al.* 1984). The model described in this paper for *Agrostemma githago* includes sufficient detail to mimic reality without the excessive proliferation of parameters that accompanies many models. This type of model might therefore be used as the basis for efficient, computer-based weed management systems, with great potential value to farmers and growers.

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