
Predicting the Determinants of Weed Abundance: A Model for the Population Dynamics of *Chenopodium album* in Sugar Beet

Author(s): R. P. Freckleton and A. R. Watkinson

Source: *Journal of Applied Ecology*, Dec., 1998, Vol. 35, No. 6 (Dec., 1998), pp. 904–920

Published by: British Ecological Society

Stable URL: <https://www.jstor.org/stable/2405146>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Applied Ecology*

Predicting the determinants of weed abundance: a model for the population dynamics of *Chenopodium album* in sugar beet

R.P. FRECKLETON and A.R. WATKINSON

Schools of Environmental and Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

Summary

1. Previously published literature on the population dynamics of a common arable weed, *Chenopodium album*, and its interactions with an arable crop, sugar beet, is reviewed with a view to (i) assessing the degree of variability in life-history traits, and (ii) parameterizing simple models of population dynamics to explore the factors determining weed abundance.

2. Comparison of previously published data sets indicates that (i) the yield–density responses of *C. album* in monoculture are remarkably consistent across sites and years; (ii) the per plant interspecific competitive effect of sugar beet on *C. album* is roughly the same as the per plant intraspecific effect of *C. album*; (iii) the allometric relationship between the seed production of *C. album* and plant biomass is invariant; and (iv) there is considerable variation in published estimates of rates of seed emergence, mortality and seedbank decay.

3. These data are used to parameterize a simple analytical model for the population dynamics of *C. album* in a rotation containing sugar beet. Sensitivity analysis indicates that the key parameters in determining changes in population size are the rates of emergence and mortality of seeds, as well as the rate of mortality of plants through control.

4. Using inferred levels of variability to compare deterministic and stochastic implementations of the model indicates that population sizes, and variability in population sizes, will be dominated by environmentally driven variations in the rate of seed germination and the rate of control.

5. From a practical perspective, these results indicate that (i) further information on the effects of control on plant numbers, and (ii) monitoring and prediction of emergence rates is likely to be the most successful approach to predicting weed numbers and levels of infestation.

6. The modelling shows how it is possible to use existing published data to parameterize simple analytical models, as well as to use information on scales of parameter variability with sensitivity analysis of such models to explore population dynamics. This provides an effective basis for exploring the impact of changing management on weed numbers in variable environments.

Key-words: stochastic model, density dependence, annual weed control, temporal variability.

Journal of Applied Ecology (1998) **35**, 904–920

Introduction

Attempts to describe and predict the population dynamics of plants such as arable weeds have tended

to be compromised by a lack of generality (e.g. Cousens & Mortimer 1995; Cousens 1995). Whilst a theoretical framework for modelling the long-term behaviour of annual plant and weed populations exists (e.g. Watkinson 1980; MacDonald & Watkinson 1981; Firbank & Watkinson 1985, 1986; Pacala 1986; Cousens *et al.* 1988; Cousens & Mortimer 1995), most predictive models have been developed almost exclus-

ively from data sets derived from one or only a few years trials.

There is a relatively long history of attempting to describe the effects of weeds on the yield of crop species (e.g. Holliday 1960; Mead 1970; Watkinson 1981; Wilson & Wright 1990). Attempts to predict the long-term behaviour of weed populations have, however, been more recent (Firbank *et al.* 1984; Cousens *et al.* 1986; Gonzalez-Andujar & Perry 1995). The basis for models predicting weed abundance are simple difference equations that relate the number of individuals emerging in one year to those emerging the previous year, through non-linear functions of densities of the crop and the weed (Firbank & Watkinson 1985). Modifications to these functions allow the role, for example, control (Cousens *et al.* 1986; Firbank & Watkinson 1986), seed pool dynamics (MacDonald & Watkinson 1981), and spatial variability and dispersal (Gonzalez-Andujar & Perry 1995) to be incorporated.

Despite the fact that simple, readily parameterized models have been successful in characterizing the dynamics of weed populations from single sites, the utility of these models in predicting dynamics has been questioned. Cousens (1995), for example, argues that such models are too simplistic and do not incorporate enough of the complex details of the relationships between plant traits and the environment to be able to describe long-term dynamics realistically. He and other authors therefore advocate the development of simulation models (e.g. Kropff 1988; Kropff & Spitters 1992; Kropff *et al.* 1992; Weaver, Kropff & Cousens 1993) that explicitly relate plant growth and competition to the environment, primarily to predict the outcome of competition within a growing season. The problem with such models, however, is that they require very intensive studies to be successfully parameterized. In addition, whilst such models have been used theoretically to analyse the causes and consequences, for example, variations in competitive ability for yield predictions, this does not mean that such models characterize the key determinants of variations in plant numbers from one year to the next. Whilst lacking the intricate detail of more complex models, the main successes of simpler population models in analysing the dynamics of weed populations have been in: (i) analysing key determinants of the invasion/persistence/eradication of weeds (e.g. Firbank & Watkinson 1986); (ii) determining key areas of the life cycle, particularly in terms of the scope for efficient control (e.g. Medd & Pandey 1993; Jordan *et al.* 1995); and (iii) in analysing and contrasting the economic viability of a range of control options (e.g. Doyle, Cousens & Moss 1986; Jones & Medd 1997).

Most attempts to model population dynamics of arable weeds are compromised by a lack of data: either data are not available over a long time period, or studies are not spatially replicated. As a consequence, previous analyses of the population dynamics of arable weeds have not been able to identify those areas

of the life-cycle that are subject to the greatest spatial or temporal variability. Sensitivity analysis on the effects of different model parameters is rarely performed and data are not available to define the expected range of variation in model parameters. Ultimately, therefore, it is not possible to state which parameters of the life-cycle play the most important role in determining year to year fluctuations in population numbers. Additionally, the lack of temporally replicated parameter estimates or stochastic estimation of the impact of temporal variability means that model results are potentially biased (Freckleton & Watkinson 1998). This lack of basic information clearly severely compromises the use of population models in weed management since it is impossible to say to what extent the results of one study will apply to others, and the spatial and temporal extent to which model results are robust (Firbank 1991).

The aim of this paper is to overcome such problems through analysing previously published data on the population dynamics of a prevalent arable weed. The rationale for this approach is that whilst detailed complete analyses of the population dynamics of arable weeds are rare, many studies will have measured the same key life-history variables at different places/times. Through quantitative comparisons of such data, combined with the analysis of population models, we are able to (i) identify areas of the life-cycle for which data are lacking; (ii) identify those variables that are subject to the greatest spatial and temporal variability; (iii) analyse the consequences of parameter variability for population sizes and hence determine the variables that are most important in driving weed population dynamics; and (iv) provide an analytical framework for exploring the effects of different management options on weed numbers. The approach is illustrated through an analysis of the population dynamics of *Chenopodium album* L., one of the most abundant and widespread arable weeds world-wide (e.g. Schroeder, Mueller-Schaerer & Stinson 1993), in a rotation containing sugar beet. This cropping scenario is typical of many systems that currently present problems to agriculture: the weed possesses a long-lived seedbank (Harrington 1972), is sufficiently closely related to the crop plant that herbicidal control may be difficult (Schweizer & May 1993), and grows very vigorously in competition with sugar beet (Kropff & Spitters 1991). Our analysis allows us to isolate those areas of the life-cycle for which detailed information and models would aid the prediction of population sizes in the long term, as well as to determine the influence of control measures on predictions of weed population dynamics.

C. album and the sugar beet rotation

Sugar beet is generally grown in a four- or five-course rotation in conjunction with cereals, potatoes, oilseed rape or set-aside/industrial break crops (Jaggard,

Limb & Proctor 1995). The sugar beet crop is sown after the first week in March, and preferably before May (Durrant, Marsh & Jaggard 1993). Recommended sowing densities correspond to around 11 plants m^{-2} , with a 20 cm plant spacing and 55 cm row spacing. Pre-emergence herbicides and NPK fertilizer (typically 70 kg ha^{-1}) are applied at the time of sowing. During growth, further herbicides and other pesticides are applied, if necessary, as well as NPK fertilizer (a further 70 kg ha^{-1}). *C. album* and other weeds may be mechanically removed by tractor hoeing. This removes all weeds between the rows of sugar beet but is, however, only an option during the early part of the growing season before the crop achieves 100% ground cover, i.e. until mid-June. The crop is harvested between October and December, with the exact timing depending on a combination of the logistics of factory processing schedules and weather suitability. *C. album* begins to shed seed during September. At the time of harvesting, *C. album* plants are simply flattened by the mechanized harvester, with the seed being ploughed into the soil when the seed bed is prepared for the next crop. Detailed descriptions of the cultivation of sugar beet in the UK are available from Jaggard, Limb & Proctor (1995). Broadly speaking the same approach is applied elsewhere (e.g. continental Europe and North America), where *C. album* and other weeds, notably *Amaranthus retroflexus*, may also be a considerable problem (e.g. Parry & Smith 1993; Thomas & Annal 1995).

During the subsequent rotation, *C. album* is generally easily controlled by a variety of broadleaf herbicides (generally applied as one pre-emergence and two post-emergence applications in sugar beet), although initial seedling establishment rates may be high in some industrial crops such as linseed (R. Freckleton, personal observation). Whilst an important weed of potatoes and other spring sown vegetable crops, it is less common in rape crops and generally absent in cereal crops (e.g. Schroeder, Mueller-Schaerer & Stinson 1993) especially when these are winter sown. In addition, *C. album* tends to compete only weakly with cereals when emergence does occur (Frantik *et al.* 1990). In the models presented below it is assumed that the sugar beet is grown in rotation with four cereal crops, and that *C. album* is unable to establish within the cereal phase of the rotation, as would be the case with winter or early sown spring crops.

Modelling the population dynamics of *C. album*

In this section we develop a simple difference equation model to describe the population dynamics of *C. album*, and infer approximate mean values for the model parameters using data derived from the literature. We use sensitivity and stochastic analyses of this model to determine the impacts of uncertainty/variability in model parameters on population dynamics and predictions of population numbers. The

aims of this analysis are to determine those parameters that impact most strongly on population dynamics, as well as to target those areas of the life-cycle for which more detailed information would improve predictions of population numbers.

In general, a model for the dynamics of an arable weed requires components to describe changes in the numbers of vegetative plants, in this case seedlings (N), and seeds (S). This requires a pair of coupled difference equations that relate the numbers of seeds and seedlings at time t to the numbers at some time in the future (e.g. MacDonald & Watkinson 1981; Cousens & Mortimer 1995):

Number of seedlings
at time $t + R$

$$= \begin{aligned} &\text{Recruitment from seeds} \\ &\text{produced at time } t \\ &+ \text{Recruitment from seeds} \\ &\text{in the soil seed bank at time } t \end{aligned}$$

Number of seeds at
time $t + R$

$$= \begin{aligned} &\text{Seeds entering soil} \\ &\text{seed bank at time } t \text{ and} \\ &\text{surviving to time } t + R \\ &+ \text{Seeds in the soil} \\ &\text{seed bank at time } t \text{ and} \\ &\text{surviving to time } t + R \end{aligned}$$

Or, more specifically,

$$N_{t+R} = g(1-m_1) p s_m N_t f(p N_t) + g(1-m_2) S_t \quad \text{eqn 1.1}$$

$$S_{t+R} = (1-m_1)(1-g) p s_m N_t f(p N_t) + (1-m_2)(1-g) S_t \quad \text{eqn 1.2}$$

Here it is assumed that plants are able to establish only at one point in an R course rotation. Equations 1.1 and 1.2 both have two components: the contribution to the numbers of individuals in either state at time $t + R$ of either seeds that were produced by weeds in the crop R years earlier, or the contribution from seeds that survived from the seed pool R years earlier. The changes in numbers are defined by the variables m_1 and m_2 that describe, respectively, the proportion of seeds produced by the previous vegetative generation that die through the rotation, and the proportion of seeds previously in the seedbank that die through the rotation; g measures the probability that a seed germinates and survives to produce a seedling; p is the proportion of plants that survive control. Note that germination of the weed during the cereal phase of the rotation can effectively be considered to increase the mortality levels of seeds as these plants typically cannot establish. We assume that this loss is negligible, however, in a rotation of winter cereals.

The parameter s_m and the function $f(pN)$ describe the seed production of the population as a function of the density of plants present. To derive these, the mean weight of plants, \bar{w} , is related to the density of seedlings present, as well as to the density of the crop by the equation (Watkinson 1981; Firbank & Watkinson 1985):

$$\bar{w} = w_m[1 + a(pN + \varepsilon B)]^{-1} \quad \text{eqn 2}$$

where a is a parameter that describes the strength of intraspecific competition between weed plants; ε is an equivalence coefficient that describes how many individuals of the weed the competitive effect of the crop is equivalent to; and w_m is the maximum mean weight of an isolated individual, i.e. in the absence of competitive effects. Note that p , the proportion of plants surviving control, is included in eqn 2, so that we may define eqn 2, and consequently plant performance, in terms of the numbers of surviving plants. In uncontrolled monocultures, $p = 1$, and $B = 0$, so that eqn 2 is defined solely in terms of w_m and a . To predict the seed production of the weed population from the weight of reproductive plants, we use an allometric relationship that predicts the seed production per plant (\bar{s}) as a function of the mean weight per plant (\bar{w}), i.e.

$$\bar{s} = c\bar{w}^k \quad \text{eqn 3}$$

Equations 2 and 3 may then be combined to yield the constant s_m ($s_m = cw_m^k$), which is the mean number of seeds produced by an isolated weed plant, and the competition function $f(pN) = [1 + a(pN + \varepsilon B)]^{-k}$, which describes the decline in seed yield as a function of the densities of the weed and the crop.

MODELLING INTRA-SPECIFIC COMPETITION AND FECUNDITY

In order to estimate the effects of intraspecific competition on the performance of plants, data (mean

shoot dry weight, with one exception) from six published field experiments were used, together with a set of data collected in 1995 from a field containing a failed crop of oilseed rape (flea beetle damage to seedlings in a late sown crop had led to widespread mortality, allowing *C. album* to dominate) at IACR Broom's Barn, UK. In each case the *C. album* was grown in monoculture. The density response has been plotted on an arithmetic scale in Fig. 1a. It is impossible from this plot to determine the degree to which the yield–density response varies across the studies. Instead it is necessary to plot the data on a logarithmic scale. For density responses of the form of eqn 2 (i.e. essentially reciprocal relationships) it is necessary to use a double logarithmic plot as simply logging one axis (which may yield an apparently sigmoid response if, for example, the density axis alone is logged) generates misleading interpretations of the response, such as apparent minimum yields at high densities. It is clear from Fig. 1 that the yield–density response in *C. album* is remarkably consistent across the seven studies, given that they span the years 1962–95 and countries as far removed from each other as Finland, New Zealand and Japan. The degree of variation at any single density is low, and generally confined to well within an order of magnitude. The only indication of systematic deviation comes from the data of Yoda *et al.* (1963) who, however, recorded the fresh weight of both shoots and roots together. We can therefore conclude that the degree of variability in time or space of the monoculture yield–density response in *C. album* is low.

The data of Yoda *et al.* (1963) indicate that some degree of density-dependent mortality occurs in populations of *C. album*. This mortality was observed in populations at densities in excess of 5000 m⁻², and these populations had failed to reach the asymptotic thinning boundary in any case (Weller 1987). Since our analysis is concerned mainly with low-density populations, we ignore density-dependent mortality through self-thinning.

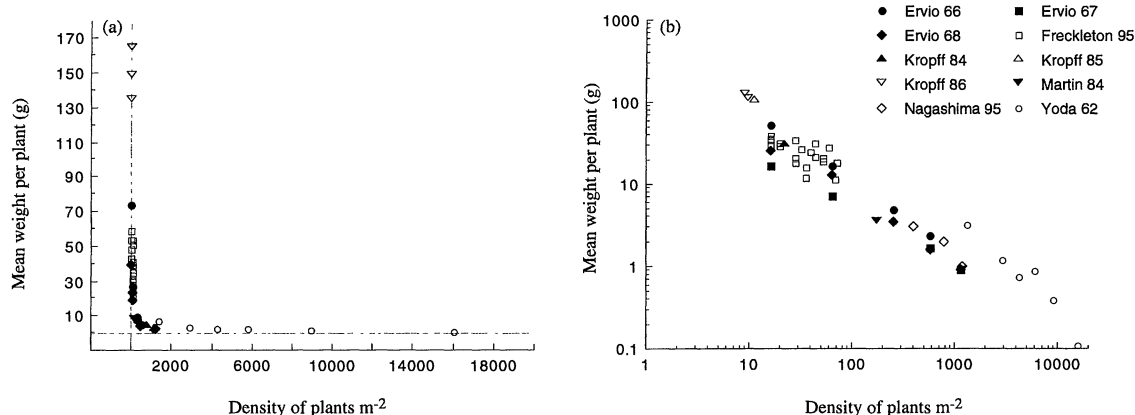


Fig. 1. Published monoculture yield–density relationships in *C. album*, showing the relationship between the mean dry weight per plant and the density of plants m⁻². The legend indicates the author of the study and the year in which the study was performed. The data from Yoda *et al.* (1963) have been averaged from 26 down to 6 points. Sources not cited in text: Nagashima & Terashima (1995), Nagashima, Terashima & Katoh (1995) and Martin (1984).

The two studies that present data on the allometric relationship between seed set and plant biomass indicate that these relationships are also relatively consistent (Fig. 2). The relationship between log seed number and log weight is linear, with little difference between the study by Erviö (1971) from Finland and that by Harrison (1990) from the USA. These two studies also have implications for the yield–density response: it should be noted from Fig. 2 that the upper bound to plant size is around 200 g per individual, which is consistent with the trend seen in Fig. 1.

Since the data in Fig. 1 are collected from monocultures, we may use the data in Fig. 1 to estimate w_m and a in eqn 2. Unfortunately, plants have not been grown at low enough densities to provide robust estimates of w_m and a through, for example, non-linear modelling. We therefore infer likely values for the parameters of eqn 3 by inspection of Figs 1 and 2, and then explore the impacts of variation and covariation in parameter estimates using a sensitivity analysis in the next section. Note that the mean weight per weed plant is reduced from $w = w_m$ at a density of $N = 0$ to $w = w_m/2$ at a density of $N = a^{-1}$. That is, a is the reciprocal of the density required to reduce the mean weight per individual from w_m to $w_m/2$. As noted above, by inspection of Figs 1 and 2 it may be inferred that the value of w_m will be between 150 g and 250 g with an approximate mean of 200 g. The value of a^{-1} must therefore lie in the range of 1–20. Taking an approximate value of $a^{-1} = 10$ gives an inferred value of $a = 0.1$.

MODELLING THE IMPACTS OF COMPETITION WITH THE CROP

In the absence of measurements of mean weight across a range of densities of both species, the impact of the sugar beet on the performance of *C. albus* was assessed by simply asking how far observed mean

weights in the presence of the crop deviate from what we would expect if there were no crop present. Only when the mean weights recorded in mixtures deviate substantially from the mean weights recorded in monoculture, when plotted against total density or monoculture density, respectively (Fig. 3), is there evidence that the equivalence coefficient from eqn 1 deviates from unity. What is clear from Fig. 3 is that there is only one case in which there is very marked deviation from the overall trend line: this is data taken from Kropff *et al.* (1992) where the germination date of the *C. albus* was experimentally manipulated to be much later than that of the crop. In the other cases, both the mean and variance about mean values are the same for the data from both mixtures and monocultures. Owing to the fact that both intra- and interspecific responses were not measured simultaneously in these studies, it is not possible to determine exact competitive effects of the crop on *C. albus* for each study. For modelling purposes a mean value of $\varepsilon = 1$ is therefore assumed in eqn 1, and the impacts of varying ε is explored using sensitivity analysis.

SEED SURVIVAL AND GERMINATION

The maximum life-span of *C. albus* seeds in the soil has been enthusiastically estimated at up to 1700 years (Ødum 1965), although in practice seeds would be expected to die much sooner. Since *C. albus* is an important weed of a variety of cropping systems world-wide, a number of studies have attempted to describe seedbank behaviour. From this literature two kinds of measures of seedbank behaviour can be distinguished: (i) recruitment rates (the numbers of seeds emerging as seedlings each year are measured as a proportion of either seeds present in the soil or seeds originally sown); and (ii) decay rates (the numbers of seeds remaining in the soil are recorded over a period of time, with this rate measuring the proportion lost

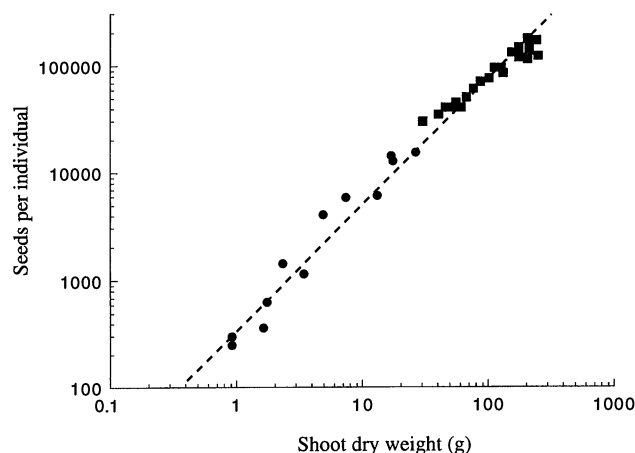


Fig. 2. Allometric relationship between seed production per individual and above ground biomass in *C. albus*. Data taken from ■ Erviö (1971) and ● Harrison (1990). The fitted line is the allometric relationship, $y = 420x^{1.19}$ ($r^2 = 0.98$; $n = 40$; $P < 0.0001$).

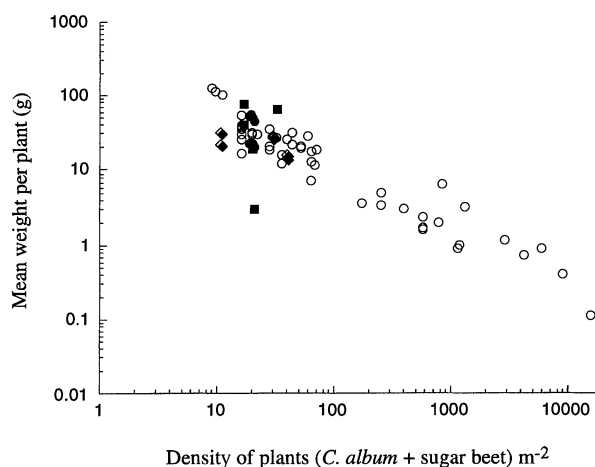


Fig. 3. The impact of competition from sugar beet on the mean performance of *C. album* plants showing the effect of increasing *C. album* density on the monoculture performance of *C. album* (○), and the effect of the combined density of *C. album* and sugar beet from competition experiments performed by: ◆ Schweizer & May (1993); ■ Kropff *et al.* (1992); ● Scott & Wilcockson (1983).

due to the combined effects of germination and mortality). Both of these rates are functions of g , the emergence rate, and m , the seed mortality rates, and therefore have to be manipulated in order to yield estimates of g and m (Rees & Long 1993).

Table 1 summarizes data from nine papers from which it was possible to estimate either one or both of these parameters. No studies have measured mortality directly, but three studies (Roberts & Feast 1973b; Forcella 1992; Forcella *et al.* 1992) have measured g , the emergence rate, directly. In these studies the density of seeds in the seedbank was estimated prior to seedling emergence, and then the numbers of seedlings emerging were recorded. The values of g estimated from these studies range between < 0.01 and 0.19 , although the values from Forcella (1992) may be inflated compared with those from Forcella *et al.* (1992) and Roberts & Feast (1973b) as the sampling depth was half that of the latter studies (10 cm vs. 20–23 cm). If we assume that most *C. album* seeds emerge from the top 5 cm of the soil (e.g. Roberts & Feast 1972) and that seeds are homogeneously distributed within the soil, then the rates from Forcella (1992) may simply be halved for comparison with those of Forcella *et al.* (1992) and Roberts & Feast (1973b). In this case the estimates from Forcella (1992) become: 0.10, 0.02, 0.02, 0.05.

We estimated the per annum seed mortality m as well as g from the data of the other seven papers. To do this it is necessary to construct equations predicting the numbers of seedlings emerging and the number of seeds remaining in the soil one year after sowing in terms of g and m , since these have not been measured directly. Over the course of one year a proportion $(1-m)$ survives mortality and a proportion $(1-g)$ do not germinate. Hence, the proportion remaining after one year is given by $(1-g)(1-m)$. Over a period of T years the proportion remaining is given by (e.g. Rees & Long 1993):

$$P_r = (1-m)^T(1-g)^T. \quad \text{eqn 4}$$

To estimate the total numbers of seedlings that have emerged over a given time period in terms of m and g , it is necessary to account for the order in which events occur during the course of a generation. The studies in Table 1 that have measured both rates of decay and rates of emergence were all initiated at the time that *C. album* plants set seed 6 months before emergence. In the first year, therefore, the proportion emerging is given by $g(1-m)^{0.5}$, if the mortality rate is assumed to be constant through the year. In the second year the proportion emerging will be $g(1-g)(1-m)^{1.5}$, and so on. After T years the total proportion of the seed to have emerged will be:

$$P_e = \sum_{t=1}^T g(1-m)^{t-0.5}(1-g)^{t-1}. \quad \text{eqn 5}$$

Given that, from eqn 4, it is possible to express either g or m in terms of P_r , and m or g , respectively, it is possible to solve eqn 5 to obtain estimates of g and m . These estimates are presented in Table 1 together with corrections of g to allow comparison of estimates taken from samples taken from different depths.

The results from this analysis indicate that there is a reasonable degree of consistency in the estimates of mortality. The values range from 0.07 to 0.25, with all but two estimates falling in the range 0.23–0.25. The estimates of emergence rates obtained both directly and indirectly are much more variable, however. The indirectly calculated values are broadly in line with those measured directly in the three studies above (range of 0.02–0.46 for the indirect values, compared with a range of < 0.01 –0.19 for the directly measured values). An assumption inherent in this procedure for estimating m and g is that seeds that attempt to germinate have the same mortality rate as seeds remaining in the seed pool. There were no significant correlations between estimates for m and those for the uncorrected g

Table 1. Rates of germination and mortality of *C. albus* seeds derived from the published literature. The table indicates the year in which the study was performed, the length of period over which rates of emergence and decay were recorded (in months) and the maximum depth to which seed densities were measured. The final two columns are estimates of the parameters *m* (per annum mortality) and *g* (per annum germination rate) obtained using the method outlined in the text where not available directly from the source. Figures in brackets indicate corrections of the germination rate to account for variations in depths of sampling between studies. Sources are: [1] Roberts & Dawkins (1967); [2] Roberts & Feast 1972; [3] Roberts & Feast 1973a; [4] Roberts & Feast (1973b); [5] Conn & Farris (1987); [6] Conn (1990); [7] Forcella 1992; [8] Forcella *et al.* 1992; [9] Lawson & Wright (1993)

	Study period	Study length (m)	Measured emergence	Measured decay	Depth (cm)	Mortality (m)	Germination (g)
[1]	1961	12	0.11	—	< 23	—	0.11
	1962	12	0.06	—	< 23	—	0.06
	1963	12	0.09	—	< 23	—	0.09
	1964	12	0.08	—	< 23	—	0.08
	1965	12	0.09	—	< 23	—	0.09
	1966	12	0.10	—	< 23	—	0.10
[2]	1963–68	60	0.77	0.98	< 2.5	0.15	0.06 (0.46)
	1963–68	60	0.48	0.95	< 7.5	0.25	0.10 (0.26)
	1963–68	60	0.51	0.94	< 15	0.23	0.20 (0.26)
	1963–68	60	0.56	0.97	< 2.5	0.25	0.04 (0.34)
	1963–68	60	0.29	0.88	< 7.5	0.25	0.05 (0.13)
	1963–68	60	0.17	0.74	< 15	0.19	0.06 (0.05)
[3]	1967	12	0.03	—	< 23	—	0.03
	1968	12	0.08	—	< 23	—	0.08
	1969	12	0.05	—	< 23	—	0.05
	1970	12	0.06	—	< 23	—	0.06
[4]	1962–70	72	0.46	0.96	< 15	0.24	0.17 (0.23)
	1962–70	72	0.14	0.47	< 15	0.07	0.02 (0.03)
[5]	1985	21	—	0.38	< 15	—	—
	1987	31	—	0.63	< 15	—	—
[6]	1988	43	—	0.74	< 15	—	—
	1989	54	—	0.46	< 15	—	—
[7]	1988	6	0.19	—	< 10	—	0.19 (0.10)
	1988	6	0.06	—	< 10	—	0.06 (0.02)
	1990	6	0.03	—	< 10	—	0.03 (0.02)
	1990	6	0.09	—	< 10	—	0.09 (0.05)
[8]	1991	6	0.07	—	< 20	—	0.07
	1991	6	< 0.01	—	< 20	—	< 0.01
	1991	6	0.10	—	< 20	—	0.10
	1991	6	< 0.01	—	< 20	—	< 0.01
	1991	6	< 0.01	—	< 20	—	< 0.01
	1991	6	0.08	—	< 20	—	0.08
[9]	1987–90	36	—	0.52	—	—	—

($r = 0.30$, $n = 8$; $P = 0.49$) and the indirectly estimated values of g ($r = 0.44$, $n = 8$; $P = 0.29$) however. There was also no correlation between the indirectly estimated and raw g estimates ($r = 0.24$, $n = 8$; $P = 0.58$) indicating that the correction had not tended to introduce a bias into the data. Note that whilst the data of

Roberts & Feast (1972) show some patterns of variability related to experimental conditions (depth of burial and cultivation), the data from Forcella (1992) and Forcella *et al.* (1992) indicate quite clearly that rates of emergence are likely to be very variable under unmanipulated conditions.

The main area of the life-cycle for which detailed data are lacking is on the effects of control practices on plant mortality. Data published in the literature are commonly derived from trials comparing the effectiveness of a variety of herbicides. It is often the case, however, that since high doses of herbicides will generally kill most or all weeds, such trials typically employ rather low application rates in order that some differences will actually be recorded. From trials conducted at Morley Research Station (UK) the 'best' rates of control recorded from single applications of herbicide in trials conducted since 1987 are: 97.4%, 89.5%, 86.6% (May & Hilton 1990); 87.1%, 85.7%, 84.3%, 84.6% (Hilton & May 1990); 95.1%, 94.8% (May 1993). It is clear that a degree of variation in these figures exists: the proportion of plants surviving control varies from 0.026 to 0.157, i.e. by nearly an order of magnitude. For three applications of herbicides (typically one application pre-emergence and two applications post-emergence, Jaggard, Limb & Proctor 1995) this gives a range of 1.8×10^{-5} – 3.8×10^{-3} , i.e. over two orders of magnitude of variation.

No data at all are available on the effects of mechanical control. If mechanical control is applied through tractor hoeing, then typically 70–90% of the soil surface may be affected, with most or all plants being removed from this area. Consequently, mechanical control may reduce the proportion of plants surviving control by a further order of magnitude. Given the uncertainty in these estimates of the parameter p that describes the effects of control, we explore a range of values of p .

Model analysis

EQUILIBRIUM POPULATIONS AND SENSITIVITY ANALYSIS

We model a five-course rotation where sugar beet is grown every fifth year, with cereals grown in the other 4 years. Since *C. album* has red–far red and light requirements for germination (Cumming 1963; Williams & Harper 1965; Karssen 1970) and ground cover is complete in cereal crops by the time *C. album* emerges, it is assumed that establishment is nil during the cereal phase of the cropping cycle. Equation 1 may therefore be modified to:

$$N_{t+5} = g(1-m)^{4.5} s_m p N_t f(p N_t) + g(1-m)^5 S_t \quad \text{eqn 6.1}$$

$$S_{t+5} = (1-m)^5 (1-g) S_t + (1-m)^{4.5} (1-g) s_m p N_t f(p N_t). \quad \text{eqn 6.2}$$

These equations have the same structure as eqns 1.1 and 1.2, with the difference lying in the values for seed mortality in the seed bank: in eqn 6.1 and 6.2 these are derived by accounting for the mortality of seeds through the entire rotation (5 years for seeds in the

seed bank; 4.5 years for seeds produced at time t). The equilibrium conditions for this model are solved by setting $N_{t+5} = N_t = N^*$ and $S_{t+5} = S_t = S^*$ and solving for N^* and S^* . This yields:

$$N^* = \frac{((p\lambda')^{1/b} - 1)}{ap} - \frac{\varepsilon B}{p} \quad \text{eqn 7}$$

where B is the density of sugar beet. λ' is the asymptotic finite rate of population increase of the *C. album* population at the stable stage distribution, and is related to the maximal rate of increase of the population ($\lambda = g s_m (1-m)^{4.5}$). This is defined by:

$$\lambda' = g s_m (1-m)^{4.5} [1 - (1-m)^5 (1-g)]^{-1}. \quad \text{eqn 8}$$

Figure 4 shows some examples of changing parameter values on equilibrium population sizes of mature plants (i.e. pN^*) at a range of control levels (p varied from 10^{-4} to 1). Decreasing the emergence rate, g , initially leads to a steady decline in population size (Fig. 4a), which becomes increasingly non-linear near the extinction threshold, with a rapid reduction in population size from very high levels to extinction over a small range of parameter values. Additionally, the effect of changing the parameter value depends on the rate of control: increasing the rate of control pushes the population closer to extinction, so that the effect of changing g on population size becomes more pronounced. In contrast, the effect of changing the seed mortality rate, m , tends to be slight across most of the range of parameter values (Fig. 4b). Only at high levels of control very near the extinction threshold does the effect of m on population size become dramatic.

Figure 4c and 4d shows the effect of changing w_m , the mean performance of an isolated individual, on population size either when w_m is varied independently of the other parameters (Fig. 4c) or when w_m is assumed to be directly correlated with the intraspecific competition coefficient, as previous studies have indicated (e.g. Watkinson 1984; $a = 0.1 (w_m/200)$; Fig. 4d). Whilst, in the former case the effect of changing w_m is very similar to the effect of changing g in Fig. 4a, in the latter case the slope of the relationship between log population size and log w_m is considerably reduced at higher parameter values. This is owing to compensation for the effect of changing w_m through changed intensity of competition; an increase in w_m is compensated for by an increase in a , leaving little overall change in population size. This is the reason why the curves in Fig. 4d are very much flatter than the corresponding curves in Fig. 4c. The effect of changing the equivalence coefficient, ε , is shown in Fig. 4e. In this case the effect of changing the value of the parameter is slight across the entire range of parameter values, except at levels of control very near the extinction threshold.

The hatched areas in Fig. 4 show the range of parameter values inferred above, and summarized in

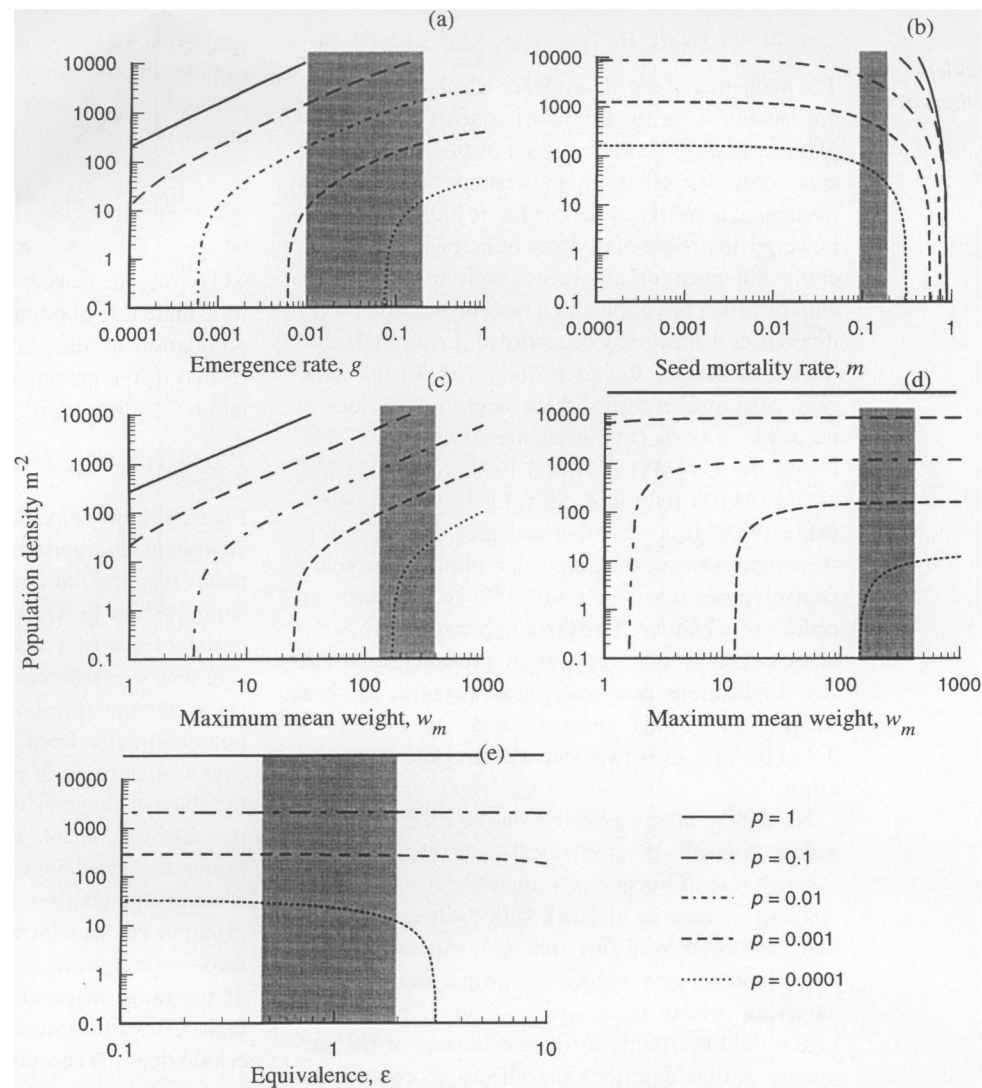


Fig. 4. Impacts on the population size predicted by the population model (eqn 8) of changing (a) the emergence rate of *C. album* seeds, g , (b) the seed mortality rate, m , (c) the maximum weight per *C. album* plant, w_m , (d) the maximum weight per *C. album* plant when this parameter is correlated with parameter a from the density response (eqn 1), and (e) the competitive equivalence coefficient for the effect of sugar beet on *C. album*. Parameter values, unless varied are as given in Table 2. The control level, p , is varied as indicated. The hatched areas indicate the likely range of mean values as given in Table 2 (see text for details).

Table 2. From inspection of Fig. 4, however, it is clear that across all values of the control parameter, p , populations always respond to changing the value of g , the emergence rate. Only when w_m is assumed not to covary with a is there a response of populations to varying w_m . In the case of the other parameters, populations tend to respond to any great degree only as the extinction threshold is approached.

In order to contrast the impacts of varying the model parameters on population size, we use a sensitivity analysis of the effects of varying parameters about their inferred mean values as the rate of control is changed. For any parameter i in eqn 6 the sensitivity index, σ_i , is defined as:

$$\sigma_i = \left| \frac{\partial \log N^*}{\partial \log i} \right| \tag{eqn 9}$$

This index measures the proportional change in the equilibrium population size with a small change in the parameter value. σ_i is scaled to be positive, i.e. the sign of the parameter is not used to record whether increasing i leads to an increase or a decrease in N^* . This index is a natural measure of the impact of parameter variation on population dynamics. This is because variation in population size will be related to temporal or spatial variance in a model parameter through the differential of the log population size with respect to the log of the parameter value (for example see Haefner 1996). Taken at the mean value of each parameter, this index allows us to contrast the relative effects of any degree of variance in model parameters.

Figure 5 shows the effect of varying the parameter values for which population sizes were plotted in Fig. 4 on the sensitivity index. The largest sensitivity values

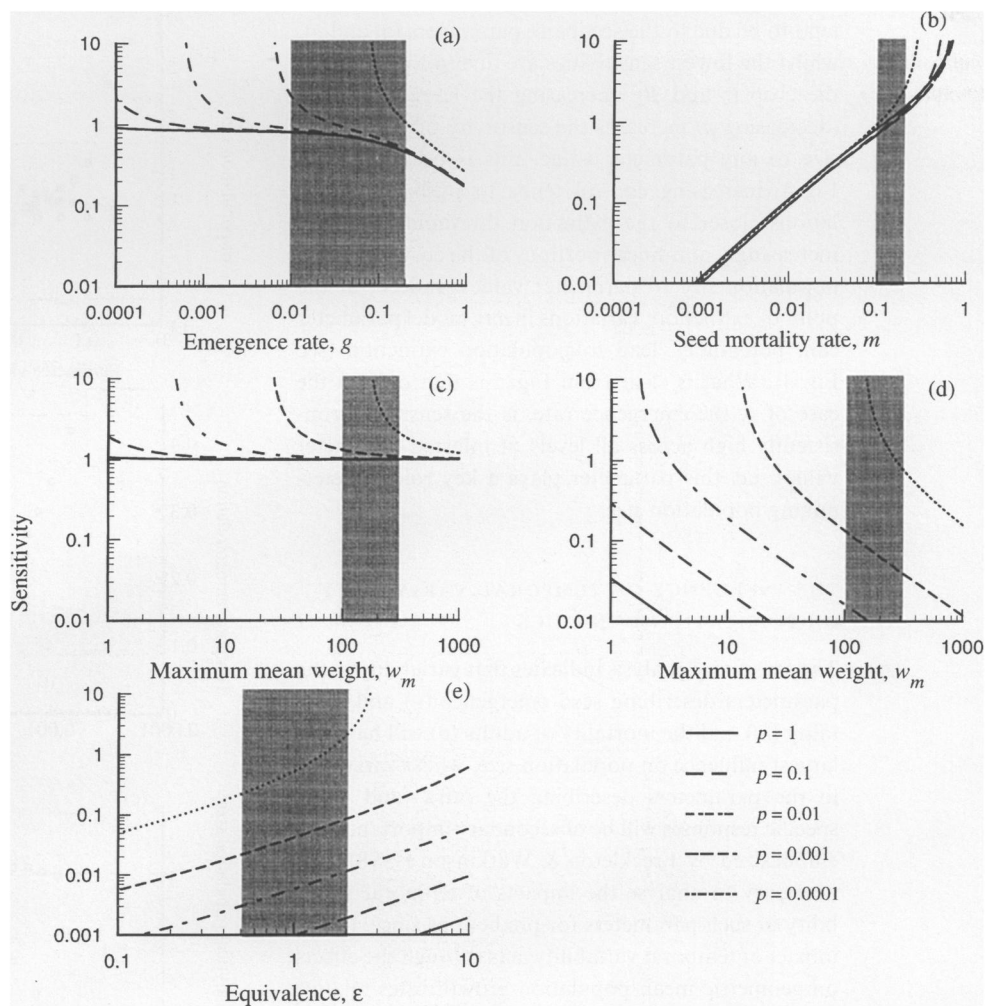


Fig. 5. Sensitivity analysis of the population size predicted by the population model (eqn 8) of changing (a) the emergence rate of *C. album* seeds, g , (b) the seed mortality rate, m , (c) the maximum weight per *C. album* plant, w_m , (d) the maximum weight per *C. album* plant when this parameter is correlated with parameter a from the density response (eqn 1), and (e) the competitive equivalence coefficient for the effect of sugar beet on *C. album*. Parameter values, unless varied, are as given in Table 2. The control level, p , is varied as indicated. The hatched areas indicate the likely range of mean values as given in Table 2 (see text for details).

Table 2. Summary of parameter values and their likely ranges of variability for the population dynamics of *C. album* inferred from analysis of published literature. The table indicates the symbol used for the parameter in the models, the mean value and the approximate range of values inferred from the range of variability observed in the data

Parameter	Definition	Mean value	Approx. range
w_m	Weight of an isolated individual (g)	200	150–250
c	Allometric constant	420	–
k	Allometric coefficient	1.19	–
a	Density response parameter	0.10	1–0.05
g	Per annum probability of seed germination	0.10	0.01–0.20
m	Per annum probability of seed mortality	0.20	0.10–0.25
ϵ	Competitive equivalence coefficient	1	0.50–1.50
B	Density of sugar beet (m^{-2})	11.11	–

tend to be due to the seedbank parameters (m and g), whilst the lowest sensitivities are due to the effects of the crop (ε and B). Increasing the level of control (decreasing p) increases the sensitivity of population size to any parameter value: this is because, as in Fig. 4, increasing control tends to push the populations closer to the extinction threshold, and into increasingly non-linear portions of the curves relating population size to parameter values. Indeed, at the point of extinction, variations in *any* model parameter can, potentially, lead to population extinction (see Fig. 4). What is clear from Fig. 5 is that only in the case of g , the emergence rate, is the sensitivity consistently high across all levels of inferred parameter values, i.e. this parameter plays a key role in determining population size.

THE INFLUENCE OF TEMPORAL VARIABILITY ON POPULATION DYNAMICS

The sensitivity analysis indicates that variability in the parameters describing seed emergence (g) and mortality (m) and the mortality of adults (p) will have the largest influence on population size, whilst variations in the parameters describing the intra- and inter-specific responses will be of secondary importance. As emphasized by Freckleton & Watkinson (1998), it is necessary to analyse the impacts of temporal variability in such parameters for predictions since: (i) the impact of temporal variability acts through the effects on geometric mean population growth rates relative to arithmetic mean changes; and (ii) the net effect of temporal variability is to bias models and over-predict population size. To explore the qualitative effects of temporal variability in the key population parameter values on predictions of population numbers, Monte Carlo simulations were performed where m , g and p were stochastically generated in each generation. Random numbers were drawn from a Beta distribution, which is a convenient distribution for modelling bounded variables. Populations were initiated at their equilibrium levels and then population sizes recorded over 100 rotations, with 500 replicates at each parameter value.

Figure 6a shows the effect on population variability of varying g or m between 0.05 and 0.6 with variance 0.01, whilst all other parameters are held constant at the mean values and $P = 0.01$ and 0.0005. As either parameter is changed, such that an extinction boundary is approached (increasing m /decreasing g), the coefficient of variation (CV) of population size increases dramatically (Fig. 6a). This effect is owing to the non-linear relationship between equilibrium population size and parameter value noted in Fig. 4. There is, however, an effect of changing the control level on the response of the CV of population size to changing m , whilst there is no effect of changing the control level on the response of population variability to changing g . This is because changing control rate

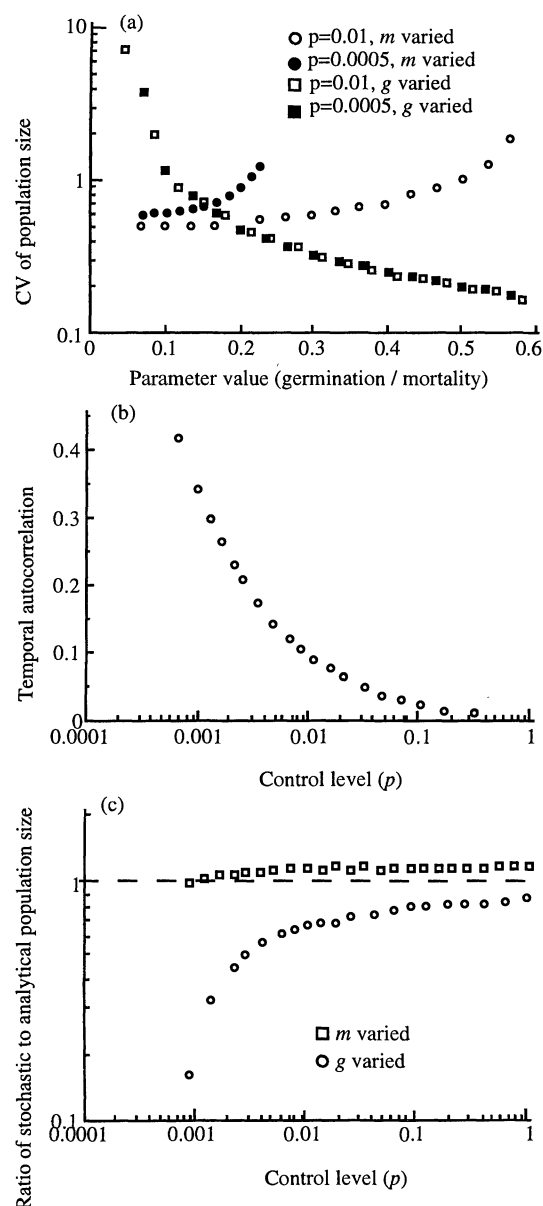


Fig. 6. Effects of temporal variability in model parameters on predicted dynamics of *C. album* populations: (a) the effect of changing mortality rate, m , and emergence rate, g , on the coefficient of variation in population size over 2000 generation simulations; (b) the effect of changing p , the proportion of plants surviving control, on the first order temporal autocorrelation coefficient for 2000 generation simulations in which g is generated randomly; and (c) the impact of variability in g and m on the ratio of population sizes estimated from the Monte Carlo simulations to that predicted by the mean model (eqn 8). Other parameters are held at their mean values (Table 2).

impacts relatively little (arithmetically) on the critical rate of germination required for population persistence, but affects the critical value of m .

In an applied context we wish to ask, given that it can be shown that population sizes may be variable in the long term, how predictable are dynamics in the short term? To explore this question the first-order autocorrelation coefficient of population size, r (e.g.

Chatfield 1996), was calculated. For simplicity, only g was generated randomly around the mean value of 0.1 and with variance of 0.01; p was varied between 0 and 1. Figure 6b shows the relationship between the value of r and p (note that p is plotted on a logarithmic scale for clarity). Increasing the level of control tends to increase the temporal autocorrelations in densities between successive generations. At low ($P > 0.1$) control levels the temporal autocorrelations are minimal. This indicates that, as control efficiency increases, population size at any point in time is increasingly dependent on the population size in the previous generation. This is because density-dependent compensation for fluctuations is weak at low control levels, i.e. when population levels are reduced/increased there is no corresponding increase/decrease in population size. Owing to the presence of the seedbank in populations of *C. album*, the lack of density dependence does not imply that density in one year is well predicted by density the previous year.

Apart from the impact of variability in parameter values on variations in population sizes, there is also an impact of parameter variability on population size itself. Figure 6c records, under varying levels of control, the ratio of the mean population size in the randomized system when either g or m was varied about its mean value to that predicted by the analytical model. At realistic (very low) values of p the effect of introducing variability into g is to decrease population sizes considerably, whilst the effect of introducing variability into m is marginally to increase population sizes. As discussed below, the reason for this is that introducing variability into the rates of g or m , whilst not affecting arithmetic mean rates, does affect geometric mean rates.

Discussion

This study has demonstrated, using analytical models parameterized from data taken from a range of sites at different times, that it is possible to: (i) generalize about the factors that play the greatest role in determining weed abundance; and (ii) predict the effects of changing parameter values, and consequently management, on weed abundance and population growth rates. Even where there is considerable uncertainty in our parameter estimates, sensitivity analysis allows the likely impact of this uncertainty to be assessed and the necessity for more accurate parameter estimation to be judged.

As noted by Cousens & Mortimer (1995), those studies that present models of population dynamics rarely use sensitivity analysis to predict the effects of changing parameter values on population size and population growth rates. This paper has attempted to overcome some of these problems by reviewing and comparing data taken from a variety of sites and dates, so as to be able to define the range of parameter space that may be expected to be observed. This, to-

gether with sensitivity analysis, provides a powerful approach for analysing the key factors determining the abundance and dynamics of arable weeds.

PATTERNS OF VARIABILITY

The data reviewed deal with: (i) the role of interactions (intra- and interspecific competition); (ii) seed production and allometric relationships; (iii) the effects of control; and (iv) patterns of dynamics in the seedbank. The approach we have taken has allowed us to determine the degree to which parameters estimated in one study are representative of other sites or other years. In the case of yield-density relationships, for example, we found that the correspondence between relationships measured at different sites or times was very good; in contrast, rates of emergence were found to be extremely variable. Individually, the studies reviewed above yield important details concerning the nature of population dynamics of *C. album*. Taken as a whole, however, we are able to go a long way towards explaining the determinants of abundance at wide temporal and spatial scales.

The strength of intra-specific interactions was remarkably consistent across all studies, as indicated by the relationship between the mean weight per individual and density observed in Fig. 1. Previous work on yield-density relationships has indicated that the parameters w_m and a of eqn 2 are primarily determined by the physical size of plants (e.g. Watkinson 1980; Lonsdale & Watkinson 1983; Firbank & Watkinson 1985) and that these two parameters are likely to be highly correlated (Watkinson 1984). Spatial or temporal variations in w_m will therefore determine the degree to which the yield-density response varies. The main sources of annual variation in yields in an agricultural system of this form would be likely to be owing to climatic variations: levels of summer rainfall and drought are the main determinants of yields of sugar beet crops (Freckleton *et al.* 1998). The results of sensitivity analysis of the model indicate that the impacts on population size of variations in the parameters w_m and a of the monoculture yield-density response on population size tend to be slight when it is realistically assumed that these parameters are positively correlated (Figs 4 and 5). Consequently, we would expect year-to-year variations in weed yields to impact only slightly on population dynamics.

Detailed experimental work (e.g. Kropff *et al.* 1987; Kropff & Spitters 1992; Kropff *et al.* 1992) has shown that, under typical agricultural conditions, *C. album* and sugar beet compete with each other mainly for light and that the outcome of competition is determined mainly by interactions occurring within the first 3 months of the growing season. Variation in the strength of interactions between the two species depends largely on relative emergence time. It is impossible for the *C. album* to emerge very much earlier than the crop; this is because the preparation

of the seed bed and the application of pre-emergence herbicides will remove all seedlings that emerge before the crop is sown. The action of the preparation of the seed bed would, however, be expected to promote further germination of *C. album* through improved soil aeration and texture. Very late germination of *C. album* seed would be unlikely since peak germination tends to occur in the warming-up period of spring (roughly mid-March to April for the UK crop; Roberts & Feast 1970; Harvey & Forcella 1993). Consequently, we would not expect the relative competitive abilities of crop and weed to vary greatly, and in any case the impacts of variation in the competitive ability of the crop on the weed (ϵ) are slight (Figs 4e and 5e).

The large number of seeds produced by *C. album* plants and the ability of these seeds to survive in the soil over long periods of time are features that clearly make *C. album* a pernicious weed of sugar beet crops (Schroeder, Mueller-Schraerer & Stinson 1993). Whilst there was little variability in the relationship between seed number and biomass in the two studies that presented data (Fig. 4), there was some degree of variation in the estimates of mean germination and mortality rates (Table 1). With one exception, all estimates of m were in the range 0.15–0.25, whereas estimates of g were considerably more variable. It is important to note that in modelling the impacts of variability in seed germination and mortality rates on population dynamics we assumed that age-specific effects were negligible, i.e. that seedbanks tend to decay exponentially over time. This assumption is partially justified since we considered a scenario in which seeds are assumed to germinate only every fifth year, so that such effects are averaged over the course of the rotation. Rees & Long (1993), however, found that seedbanks of some species do not always decay exponentially and this potentially has important consequences for predicting the outcome of control on population dynamics if significant numbers of seeds persist for a long time in the seed pool.

Since the emergence stage of the life-cycle was identified as being most important in determining year-to-year changes in population numbers, models that attempt to relate establishment to annual variations in environmental conditions will be most successful in characterizing changes in levels of weed infestation. A variety of such models have been developed (Murdoch, Roberts & Goedert 1989; Harvey & Forcella 1993; Grundy, Mead & Bond 1996), although few data are available from which to judge their success. Further developments will also have to take account of the effects on weed establishment of interactions between the effects of environmental variability and management, specifically the timing of seedbed preparation.

The limited data on the efficacy of control that were available (unfortunately from only a single site) indicated that the proportion of plants removed may vary by over an order of magnitude. The effectiveness

of an application of herbicide is known to be affected by factors including rain, wind, temperature, crop stage and the configuration of the sprayer (Jaggard, Limb & Proctor 1995). It would seem likely, therefore, that some degree of variability would occur in the mean rate of control. The analysis presented here indicates that understanding this variation is critical. Additionally, the strategy of control may be of importance: Wallinga & van Oijen (1997), for example, have shown that when control is increased in years of high weed abundance (such as a farmer increasing the amount of herbicides applied when a problem is perceived), the consequences for population dynamics may be profound and in particular may tend to stabilize dynamics, in terms of effectively bounding the range over which populations fluctuate. The role of control in the population dynamics of *C. album* and other arable weeds therefore requires more attention.

MODEL DYNAMICS

Whilst the analysis of the field data allows the range of values for different parameters to be estimated, this information is not enough to reveal the likely importance of these variations on long-term patterns of abundance. To do this it is necessary to construct models and explore the degree to which parameter variations affect population dynamics. The models used above are probably the simplest that could be constructed for the dynamics of this system: nevertheless, nine parameters have to be estimated.

The sensitivity analysis used here allows the effect of changing the value of all of the parameters on population size to be compared and hence for the relative importance of variability in each of the parameters to be assessed. This analysis indicated that variations in the rates of germination, mortality and control always exert a larger influence on population size than variations in the strengths of competitive interactions (Fig. 5). The analysis also indicated that increasing the efficiency of control increased the sensitivity of the population to variations in any parameter (Fig. 5).

In order to predict population dynamics in a temporally varying environment it is necessary to consider the impacts of variability on geometric mean population growth rates (Cohen 1966, 1993; Lewontin & Cohen 1969; Freckleton & Watkinson 1998) and particularly to consider the shape of the curve relating population size or population growth rate to changing parameter value (Freckleton & Watkinson 1998). Since such curves tend to be highly non-linear (e.g. Fig. 4), the effects on population size of either increasing or decreasing the value of a parameter do not tend to be equal. This is clearly demonstrated by the patterns of sensitivity in Fig. 5. The consequence of this asymmetry is that variance around arithmetic mean parameter values will tend either to increase or decrease population sizes, depending on whether

increasing the value of a parameter increases or decreases population size, respectively. Given the patterns observed in Fig. 5, where increasing the values of most parameters tends to increase population sizes, we would expect temporal variability to decrease population sizes relative to the predictions of equilibrium models. Additionally, the positive and negative effects of parameter variability do not compensate for each, owing to the kind of non-linearities in Fig. 4 (Freckleton & Watkinson 1998). The consequence of this, in Fig. 6c for example, is that the decrease in population size owing to variability in g tends to be greater than the increase in population size owing to variability in m . Since variability in the germination rate, g , and the rate of control, p , were identified as being key variables in population dynamics, variability in both of these can be expected to decrease population sizes. Overall, we would therefore expect population growth rates of *C. album* to be lower than would be predicted by equilibrium models that ignore the consequences of temporal variability.

The impacts of variability on population dynamics result from a loss of density-dependent control as populations approach an extinction boundary, due to the effects of increasing levels of control on population growth rate curves (Figs 4 and 5). Perhaps counterintuitively, therefore, the effect of increasing the effectiveness of control (i.e. pushing populations into the density-independent phase of population growth) is to increase temporal autocorrelations in population size. The reason for this is that density dependence compensates population growth for variations in parameter values and hence reduces the dependence of population size in one year on that in the previous year. This lack of responsiveness to changes in parameter values results from an increase in the importance of the deterministic elements in the models. In particular, the effects of parameter variation on population variability (Fig. 6a) and population size (Fig. 6c) become less important as population size increases.

In an analysis of the dynamics of 12 species commonly occurring in the Broadbalk experiment, Firbank (1993) found a weak correlation between seedbank longevity and population variability, such that species with a short-lived seedbank exhibited lower levels of year-to-year population size variability. This analysis was based solely on census data, hence it was impossible to disentangle the various correlates of seedbank persistence. In particular, it was not possible to disentangle the effects of variability in germination rates and seed mortality rates. Other correlates of seedbank persistence may also exist: for example, species with long-lived seedbanks are commonly small-seeded and hence may be most sensitive to competition (e.g. Rees 1995, 1996). Our analysis indicates that emergence rates are, in relative terms, the most variable component of the life-cycle; and the model

indicates that population size is most sensitive to variations in emergence rates. The structure of our model would be expected to be similar for most arable weeds that possess a long-lived seedbank. We would, therefore, expect model dynamics to be similar for these species, with variations in emergence and establishment rates playing the dominant role in determining population sizes.

APPLICATIONS

The model and analysis presented here (see also Jordan *et al.* 1995; Rees & Paynter 1997) attempt to: (i) collate all pre-existing information available on population dynamics and control of *C. album*; and (ii) make best use of this information by analysing it within a modelling framework. The model used is sufficiently general that, if additional information becomes available, the parameter values or model structure may be modified accordingly. This contrasts with most exercises in modelling weed population dynamics, where parameters from other studies tend to be used only when they cannot be estimated locally (see Cousens & Mortimer 1995). This exercise could easily be repeated for a range of common weeds for which large amounts of information are available, particularly in relation to seedbank behaviour (Thompson *et al.* 1998). Moreover, simple models of this sort that capture the key features of the population dynamics of arable weeds are ideal for inclusion in multidisciplinary projects, such as bio-economic modelling (e.g. Doyle, Cousens & Moss 1986; Jones & Medd 1997) as well as the development of decision support systems (Costanza *et al.* 1993; Cox 1996).

In the case of the population dynamics of *C. album* in sugar beet, this scoping exercise allows us to state that predictions of population dynamics will benefit from improved systems for predicting germination behaviour; that controlling weed populations through managing the competitive ability of the crop (e.g. Lotz, Groenvelde & de Groot 1991) will be effective only if very large changes in the competitive effect of sugar beet on *C. album* can be achieved; similarly, that alternative management options, such as biological control (Scheepens *et al.* 1997) will have to achieve large impacts on plant performance to impact severely on plant numbers; and that population dynamics are likely to be very similar in nature over a wide range of sites, although population sizes will be very variable owing to the weakening in density-dependent control of population growth at low population levels. In terms of future developments, the lack of detailed demographic data on control measures has been highlighted, and is a clear problem with specifically evaluating the effectiveness of different management regimes. In particular, with a movement towards

reducing inputs in agricultural systems and the concomitant development of new control measures, we have highlighted the requirement for detailed demographic data on the effects of such measures. Since our analysis is based on a wide range of pre-existing studies, these conclusions summarize the state of our understanding of this system, as well as highlighting specific areas for future developments. This would not have been possible using data derived from a short-term experiment conducted at a single site.

Acknowledgements

RPF would like to thank IACR Broom's Barn and the University of East Anglia for financial support. Mark Lonsdale and two anonymous referees provided helpful comments on a previous version of this manuscript.

References

- Chatfield, C. (1996) *The Analysis of Time Series*. Chapman & Hall, London.
- Cohen, D. (1966) Optimizing reproduction in randomly varying environments. *Journal of Theoretical Biology*, **12**, 119–129.
- Cohen, D. (1993) Fitness in random environments. *Adaptations in Stochastic Environments* (ed. J. Yoshimura & C. Clark), pp. 8–25. Springer-Verlag, Berlin.
- Conn, J.S. (1990) Seed viability and dormancy of 17 weed species after burial for 4.7 years in Alaska. *Weed Science*, **38**, 134–138.
- Conn, J.S. & Farris, M.L. (1987) Seed viability and dormancy of 17 weed species after 21 months in Alaska. *Weed Science*, **35**, 524–529.
- Costanza, R., Waigner, L., Folke, C. & Mäler, K.-G. (1993) Modelling complex ecological economic systems. *BioScience*, **438**, 545–555.
- Cousens, R. (1995) Can we determine the intrinsic dynamics of real plant populations? *Functional Ecology*, **9**, 15–20.
- Cousens, R., Doyle, C.J., Wilson, B.J. & Cussans, G.W. (1986) Modelling the economics of controlling *Avena fatua* in winter wheat. *Pesticide Science*, **17**, 1–12.
- Cousens, R., Firbank, L.G., Mortimer, A.M. & Smith, R.G.R. (1988) Variability in the relationship between crop yield and weed density for winter wheat and *Bromus sterilis*. *Journal of Applied Ecology*, **25**, 1033–1044.
- Cousens, R. & Mortimer, A.M. (1995) *Dynamics of Weed Populations*. Cambridge University Press, Cambridge.
- Cox, P.G. (1996) Some issues in the design of agricultural decision support systems. *Agricultural Systems*, **52**, 355–381.
- Cumming, B.C. (1963) The dependence of germination on photoperiod, light quality, and temperature in *Chenopodium spp.* *Canadian Journal of Botany*, **41**, 1211–1233.
- Doyle, C.J., Cousens, R. & Moss, S.R. (1986) A model of the economics of controlling *Alpecurus myosuroides* Huds. in winter wheat. *Crop Protection*, **5**, 143–150.
- Durrant, M.J., Marsh, S.J. & Jaggard, K.W. (1993) Effects of seed advancement and sowing date on establishment, bolting and yield of sugar beet. *Journal of Agricultural Science*, **121**, 333–341.
- Erviö, L. (1971) The effect of intra-specific competition on the development of *Chenopodium album* L. *Weed Research*, **11**, 124–134.
- Firbank, L.G. (1991) Interactions between weeds and crops. *The Ecology of Temperate Cereal Fields* (eds L. G. Firbank, N. Carter, J. F. Darbyshire, G.R. Potts), pp. 209–231. Blackwell Scientific Publications, Oxford.
- Firbank, L.G. (1993) Short-term variability of plant populations within a regularly disturbed habitat. *Oecologia*, **94**, 351–355.
- Firbank, L.G., Manlove, R.J., Mortimer, A.M. & Putwain, P.D. (1984) The management of grass weeds in cereal crops, a population biology approach. *Proceedings of the 7th International Symposium on Weed biology, Ecology and Systematics*, pp. 375–384. European Weed Research Society, Paris.
- Firbank, L.G. & Watkinson, A.R. (1985) On the analysis of competition within two-species mixtures of plants. *Journal of Applied Ecology*, **22**, 503–517.
- Firbank, L.G. & Watkinson, A.R. (1986) Modelling the population dynamics of an arable weed and its effects upon crop yield. *Journal of Applied Ecology*, **23**, 147–159.
- Forcella, F. (1992) Prediction of weed seedling densities from buried seed reserves. *Weed Research*, **32**, 29–38.
- Forcella, F., Wilson, R.G., Renner, K.A., Dekker, J., Harvey, R.G., Alm, D.A., Buhler, D.D. & Cardina, J. (1992) Weed seedbanks of the US corn belt: magnitude, variation, emergence and application. *Weed Science*, **40**, 636–644.
- Frantik, T., Kovab, P., Dostalek, J., Koblihovala, H. & Stejskalova, H. (1990) Interactions of two species of the genus *Chenopodium* with two production plants – sugar beet and spring wheat. *Folia Geobotanica et Phytotaxonomica*, **25**, 137–144.
- Freckleton, R.P. & Watkinson, A.R. (1998) How does temporal variability affect predictions of weed population numbers? *Journal of Applied Ecology*, **35**, 340–344.
- Freckleton, R.P., Watkinson, A.R., Webb, D.J. & Thomas, T.H. (1998) Yield of sugar beet in relation to weather and nutrients. *Agricultural and Forest Meteorology* in press.
- Gonzalez-Andujar, J.L. & Perry, J.N. (1995) Models for the herbicidal control of the seed bank of *Avena sterilis*: the effects of spatial and temporal heterogeneity and of dispersal. *Journal of Applied Ecology*, **32**, 578–587.
- Grundy, A.C., Mead, A. & Bond, W. (1996) Modelling the effect of weed-seed distribution in the soil-profile on seedling emergence. *Weed Research*, **36**, 375–384.
- Haefner, J.W. (1996) *Modelling Biological Systems*. Chapman & Hall, London.
- Harrington, J.F. (1972) Seed storage longevity. *Seed Biology*, Vol. III (ed. T.T. Kozlowski), pp. 145–245. Academic Press, New York.
- Harrison, S.K. (1990) Interference and seed production by common lambsquarters (*Chenopodium album* L.) in soybeans (*Glycine max*). *Weed Science*, **38**, 113–118.
- Harvey, S.J. & Forcella, F. (1993) Vernal seedling emergence model for common lambsquarters (*Chenopodium album*). *Weed Science*, **41**, 309–316.
- Hilton, J.G. & May, M.J. (1990) Sugar beet: 'fire brigade' control of large broad-leaved weeds, 1987–89. *82nd Annual Report, Morley Research Station, UK*, pp. 45–55.
- Holliday, R. (1960) Plant population and crop yield. *Nature*, **186**, 22–24.
- Jaggard, K.W., Limb, M. & Proctor, G.H. (1995) *Sugar Beet: a Grower's Guide*. Sugar Beet Research and Education Committee, London.
- Jones, R. & Medd, R. (1997) Economic analysis of integrated management of wild oats involving fallow, herbicide and crop rotational options. *Australian Journal of Experimental Agriculture*, **37**, 683–691.
- Jordan, N., Mortensen, D.A., Prenzlow, D.M. & Cox, K.C. (1995) Simulation analysis of crop rotation effects on weed seedbanks. *American Journal of Botany*, **82**, 390–398.
- Karssen, C.M. (1970) The light promoted germination of the

- seeds of *Chenopodium album* L. III. Effect of the photoperiod during growth and development of the plants on the dormancy of the produced seeds. *Acta Botanica Neerlandica*, **19**, 81–94.
- Kropff, M.J. (1988) Modelling the effects of weeds on crop production. *Weed Research*, **28**, 465–471.
- Kropff, M.J., Joenje, W., Habekote, B., van Oene, H. & Werner, R. (1987) Competition between a sugar beet and populations of *Chenopodium album* L. & *Stellaria media* L. *Netherlands Journal of Agricultural Science*, **35**, 525–528.
- Kropff, M.J. & Spitters, C.J.T. (1991) A simple model of crop loss by weed competition from early observations on relative leaf area of the weeds. *Weed Research*, **31**, 97–105.
- Kropff, M.J. & Spitters, C.J.T. (1992) An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. I. Model description and parameterization. *Weed Research*, **32**, 437–450.
- Kropff, M.J., Spitters, C.J.T., Schnieders, B.J., Joenje, W. & DeGroot, W. (1992) An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. II. Model evaluation. *Weed Research*, **32**, 451–463.
- Lawson, H.M. & Wright, G.M. (1993) Seedbank persistence of five arable weed species in autumn sown crops. *Proceedings of the Brighton Crop Protection Conference*, pp. 305–310. British Crop Protection Council, Farnham, Surrey.
- Lewontin, R.C. & Cohen, D. (1969) On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences (USA)*, **62**, 1056–1060.
- Lonsdale, W.M. & Watkinson, A.R. (1983) Plant geometry and self-thinning. *Journal of Ecology*, **71**, 285–297.
- Lotz, L.A.P., Groenvelde, R.M.W. & de Groot, N.A.M.A. (1991) Potential for reducing herbicide inputs in sugar beet by selecting early closing cultivars. *Proceedings of the Brighton Crop Protection Conference*, pp. 1241–1248. British Crop Protection Council, Farnham, Surrey.
- MacDonald, N. & Watkinson, A.R. (1981) Models of an annual plant population with a seedbank. *Journal of Theoretical Biology*, **93**, 643–653.
- Martin, M.P.L.D. (1984) Interference of fathen (*Chenopodium album*) with lucerne (*Medicago sativa*) during establishment. *New Zealand Journal of Agricultural Research*, **27**, 593–596.
- May, M.J. (1993) Comparison of pre-emergence herbicides, 1989–92, *85th Annual Report, Morley Research Station, UK*, pp. 69–78.
- May, M.J. & Hilton, J.G. (1990) The use of additives with post emergence herbicides, 1987–89. *82nd Annual Report, Morley Research Station, UK*, pp. 32–44.
- Mead, R. (1970) Plant density and crop yield. *Applied Statistics*, **19**, 64–81.
- Medd, R.W. & Pandey, S. (1993) *Compelling grounds for controlling seed production in Avena species (wild oats)*. 8th EWRS Symposium, Braunschweig, pp. 769–776. European Weed Research Society, Paris.
- Murdoch, A.J., Roberts, E.H. & Goedert, C.O. (1989) A model for germination responses to alternating temperatures. *Annals of Botany*, **63**, 97–111.
- Nagashima, H. & Terashima, I. (1995) Relationships between height, diameter and weight distributions of *Chenopodium album* plants in stands: effects of dimension and allometry. *Annals of Botany*, **75**, 181–188.
- Nagashima, H., Terashima, I. & Katoh, S. (1995) Effects of plant density on frequency distributions of plant height in *Chenopodium album* stands: analysis based on continuous monitoring of the height-growth of individual plants. *Annals of Botany*, **75**, 173–180.
- Ødum, S. (1965) Germination of ancient seeds; floristical observations and experiments with ancient seeds. *Dansk Botanisk Arkiv*, **24**, 1–70.
- Pacala, S.W. (1986) Neighbourhood models of plant population dynamics. 2. Multi-species models of annuals. *Theoretical Population Biology*, **29**, 262–292.
- Parry, D. & Smith, J. (1993) Beet growing in Italy – some of the problems. *British Sugar Beet Review*, **61**, 33–34.
- Rees, M. (1995) Community structure in sand dune annuals: is seed weight a key quantity? *Journal of Ecology*, **83**, 857–864.
- Rees, M. (1996) Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London Series B*, **351**, 1299–1308.
- Rees, M. & Long, M.J. (1993) The analysis and interpretation of seedling recruitment curves. *American Naturalist*, **141**, 233–262.
- Rees, M. & Paynter, Q. (1997) Biological control of scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology*, **34**, 1203–1221.
- Roberts, H.A. & Dawkins, P.A. (1967) Effect of cultivation on the numbers of viable weed seeds in soil. *Weed Research*, **7**, 290–301.
- Roberts, H.A. & Feast, P.M. (1970) Seasonal distribution of emergence in some annual weeds. *Experimental Horticulture*, **21**, 36–41.
- Roberts, H.A. & Feast, P.M. (1972) Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research*, **12**, 316–324.
- Roberts, H.A. & Feast, P.M. (1973a) Changes in the numbers of viable weed seeds in soil under different regimes. *Weed Research*, **13**, 298–303.
- Roberts, H.A. & Feast, P.M. (1973b) Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *Journal of Applied Ecology*, **10**, 133–143.
- Scheepens, P.C., Kempenaar, C., Andreasen, C., Eggers, T.H., Netland, J. & Vurro, M. (1997) Biological control of the annual weed *Chenopodium album* with emphasis on the application of *Ascochyta caulina* as a microbial herbicide. *Integrated Pest Management Reviews*, **2**, 71–76.
- Schroeder, D., Mueller-Schaerer, H. & Stinson, C.S.A. (1993) A European weed survey in 10 major crop systems to identify targets for biological control. *Weed Research*, **33**, 449–458.
- Schweizer, E.E. & May, M.J. (1993) Weeds and weed control. *The Sugar Beet Crop: Science Into Practice*. (eds D.A. Cooke & R.K. Scott), pp. 485–519. Chapman & Hall, London.
- Scott, R.J. & Wilcockson, S.J. (1983) Weed biology and the growth of sugar beet. *Annals of Applied Biology*, **83**, 331–335.
- Thomas, T.H. & Annal, G. (1995) Sugar beet production in the Ukraine. *British Sugar Beet Review*, **63**, 27–31.
- Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the NW European flora. *Journal of Ecology*, **86**, 163–170.
- Wallinga, J. & van Oijen, M. (1997) Level of threshold weed density does not affect the long-term frequency of weed control. *Crop Protection*, **16**, 273–278.
- Watkinson, A.R. (1980) Density-dependence in single-species populations of plants. *Journal of Theoretical Biology*, **83**, 345–357.
- Watkinson, A.R. (1981) Interference in pure and mixed populations of *Agrostemma githago*. *Journal of Applied Ecology*, **18**, 967–976.
- Watkinson, A.R. (1984) Yield–density relationships: the influence of resource availability on growth and self-thinning in populations of *Vulpia fasciculata*. *Annals of Botany*, **53**, 469–482.
- Weaver, S.E., Kropff, M.J. & Cousens, R. (1993) A simu-

- lation model of *Avena fatua* L. (wild-oat) growth and development. *Annals of Applied Biology*, **122**, 537–554.
- Weller, D.E. (1987) A reevaluation of the $-3/2$ power rule of plant self-thinning. *Ecological Monographs*, **57**, 23–43.
- Williams, J.T. & Harper, J.L. (1965) Seed polymorphism and germination. *Weed Research*, **5**, 141–150.
- Wilson, B.J. & Wright, K.J. (1990) Predicting the growth and competitive effects of annual weeds in wheat. *Weed Research*, **30**, 201–211.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University*, **14**, 107–129.

Received 16 April 1997; revision received 16 November 1998