Session 4B

Biology and Ecology of Weed Seeds

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WEED SEED PRODUCTION AS AFFECTED BY CROP DENSITY AND NITROGEN APPLICATION

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ABSTRACT

Seed production of eight weed species grown in combination with winter wheat was estimated using techniques which differed between species. Linear relationships were found between seed production and the dry weight of weeds. Crop density was an important factor in limiting seed production in all weed species. Nitrogen fertiliser doubled or trebled seed production in *Avena fatua* and *Galium aparine*, but had little effect on that of *Lamium purpureum*, *Papaver rhoeas*, *Tripleurospermum inodorum*, *Veronica hederifolia*, *Veronica persica* and *Viola arvensis*.

INTRODUCTION

Annual changes in weed populations are governed by the production and fate of weed seeds. Such changes need to be understood in relation to low-input systems, where there may be a greater risk of weeds seeding and population build-up. The number of seeds produced is an important factor in governing potential population build-up (Harper, 1977). It is important to devise methods with which the production of weed seeds can be monitored; these need to be practicable without sacrificing too much precision in determining seed numbers per plant.

In the work reported here, eight weed species were studied to estimate their seed production in the absence of a crop or in winter wheat planted at different densities, and at a range of nitrogen fertiliser applications.

MATERIALS AND METHODS

Seed production was estimated for weeds established within field experiments (1988-1992) designed to study the influence of crop density and nitrogen fertiliser on weed competition in winter wheat (Wilson *et al*, 1988, Wright & Wilson 1992). Experiments were all of similar design; a split plot fully randomised block with four replicates.

In 1988 and 1989, each replicate consisted of three crop densities and no crop as the main plots. These were split into 18 sub-plots, six for each weed species, of which one was used to study weed seed production. The species studied were *Lamium purpureum*, *Papaver rhoeas* and *Viola arvensis*.

In the 1990 and 1991 nitrogen experiments, each replicate consisted of four rates of nitrogen fertiliser as main plots, split into two sub-plots of *Avena fatua* or *Galium aparine*. In 1992, each replicate consisted of eight main plots with four rates of nitrogen fertiliser each at two crop densities, split into ten sub-plots and nine weed species plus one weed-free. In each sub-plot, areas were reserved for weed seed production and weed biomass.

In the autumn, weed seeds were sown by hand onto the seedbed and incorporated into the soil when the wheat was drilled. Crop seedlings were counted on the central m^2 of each plot in the autumn to give mean crop densities for each experiment (Table 1). The 1988 and 1989 experiments received standard fertiliser applications. In 1990-1992, nitrogen fertiliser treatments of 0, 50, 100 and 200 kg/ha N were applied in March or April. All experiments received standard fungicide treatments.

Table 1. Dates of husbandry operations, crop densities and varieties

	1988	1989	1990	1991	1992
Weeds sown	25/09/87	21/09/88	26/09/89	20/09/90	04/10/91
Crop sown	29/09/87	22/09/88	27/09/89	22/09/90	04/10/91
Wheat cultivar	Avalon	Avalon	Mercia	Mercia	Mercia
Wheat density	0	0	243	187	60
(plants/m^2)	40	45			195
	114	115			
	207	189			
Nitrogen applied	15/04/88	31/03/89	23/03/90	19/04/91	03/04/92

In February, sown weeds in the areas reserved for seed production were thinned to four plants/m^2 and naturally occurring species were removed. In March/April either four or six plants on each plot were labelled for subsequent assessment of seed production and dry weight. These selected plants were removed from the field just before seed shedding (Table 2), and seed numbers assessed. Dry weights of individual weed plants were recorded and related to the estimated seed number per plant.

Table 2. Dates of assessment of seed production

Weed species	1988	1989	1990	1991	1992
A. fatua	-	-	11/7	8/7	2/7
G. aparine	-	-	18/7	30/7	-
L. purpureum	2/6	24/5	-	-	-
P. rhoeas	20/7	10/7	-	-	16/7
T. inodorum	-	-	-	-	4/8
V. hederifolia	-	-	-	-	12/5
V. persica	-	-	-	-	27/5
V. arvensis	15/6	19/6	-	-	25/6

Methods of seed estimation

Avena fatua. Panicles were removed from each plant, counted and weighed. The number of seeds/g fresh weight of panicle, obtained from a separate sample of 80 panicles, was used to derive an estimate of number of seeds per plant.

Galium aparine. Selected plants were left to mature in paper bags, after which they were weighed and the seeds separated and counted.

Lamium purpureum. The number of flowering whorls on each branch of the labelled plants was counted. The numbers of capsules per whorl were derived from a separate sample of 80 branches. Each capsule contained four seeds, giving number of seeds per whorl, which was then multiplied by the number of whorls on each of the selected plants to give numbers of seeds per plant.

Papaver rhoeas. Capsules were removed, counted, dried and the total dry weight of capsules per plant obtained. Capsule size varied, so seed number was based on capsule weight. From a separate sample of 30 capsules, individual capsule dry weights and seed dry weights in each capsule were obtained and numbers of seeds calculated for each capsule (1000 seeds weighed 0.092 g, 0.085 g, and 0.108 g in 1988, 1989 and 1992, respectively). Average number of seeds per capsule and per g dry weight of capsule was calculated. Number of seeds per plant was derived from total dry weight of capsules per plant multiplied by number of seeds per g dry weight of capsule.

Tripleurospermum inodorum (syn *Matricaria perforata*). The number of seed heads was counted on each plant. Numbers of seeds per head were obtained from a separate sample of 20 flowering heads. Number of seeds per plant was based on the product of seeds per head and number of heads per plant.

Veronica hederifolia, Veronica persica and Viola arvensis. Numbers of capsules on each plant were counted. A random sample of 20 capsules was assessed for number of seeds per capsule. Number of seeds per plant was based on the product of seeds per capsule and number of capsules per plant.

RESULTS

Weed seed estimation and plant dry weight

The parameters for estimating seed production for each species (Table 3) showed close agreement between years. Highly significant linear relationships were found between number of seeds and dry weight per plant for all species studied (Table 4). Although the relationship was significant for *L. purpureum* in 1989, it only accounted for a small proportion of the variability. The remaining variability may be related to slug damage before assessment.

Table 3. Parameters for estimation of seed number

Parameter	Species	1988	1989	1990	1991	1992
Seeds/g dry wt of panicle	*A. fatua*	-	-	35.6	30.1	36.7
Seeds/whorl	*L. purpureum*	47.7	45.1	-	-	-
Seeds/g dry wt of capsule	*P. rhoeas*	6221	6542	-	-	5607
Seeds/flowering head	*T. inodorum*	-	-	-	-	143.1
Seeds/capsule	*V. hederifolia*	-	-	-	-	3.0
	V. persica	-	-	-	-	16.1
	V. arvensis	45.6	57.6	-	-	32.7

Effects of crop density on weed seed production

The lowest crop densities reduced seed production (mean of two years) by 85% (*L. purpureum*), 95% (*P. rhoeas*) and 92% (*V. arvensis*) compared with seeds produced in the absence of crop (Table 5). Increasing crop density resulted in a progressive decrease in weed seed production with seeds/plant approximately halved as crop density doubled.

All species studied in 1992 (Table 6) produced more seeds per plant at low as compared with high crop density, with seed production at least doubled, except for *V. hederifolia*. *V. arvensis* showed the largest response with more than a four-fold increase as crop density reduced.

Table 4. Relationships between seed production and dry weight

		Regression coefficient		% variance accounted
Species		seeds/g	s.e.	for (adjusted for d.f.)
A. fatua	1990	18.4	0.31	93% ***
	1991	22.8	0.36	94% ***
	1992	28.7	0.43	96% ***
G. aparine	1990	20.9	0.73	82% ***
	1991	24.4	0.90	70% ***
L. purpureum	1988	485	17.1	81% ***
	1989	406	23.9	29% ***
P. rhoeas	1988	1122	46.9	84% ***
	1989	970	44.9	78% ***
	1992	1282	36.1	94% ***
T. inodorum	1992	789	26.7	92% ***
V. hederifolia	1992	186	6.1	76% ***
V. persica	1992	936	23.4	93% ***
V. arvensis	1988	312	13.4	69% ***
	1989	547	22.7	75% ***
	1992	435	21.8	86% ***

Table 5. Effect of crop density on numbers of weed seeds per plant

	1988	Crop plants/m^2				1989	Crop plants/m^2			
	0	40	114	206	s.e.d.*	0	45	115	189	s.e.d*
L. purpureum	27634	4594	2022	1075	460.9	18729	2359	1655	1394	362.3
P. rhoeas	531273	41059	12442	6221	3758.8	823065	8158	3441	2140	1644.2
V. arvensis	8944	967	562	354	36.0	32309	1576	581	390	189.0

* s.e.d. values relate to crop populations excluding zero density

Table 6. Effect of crop density on numbers of weed seeds per plant in 1992. (mean of four nitrogen levels)

Species	Crop plants/m^2 60	195	s.e.d.
A. fatua	1317	636	139.8
P. rhoeas	67915	25324	10508.5
T. inodorum	7177	3316	1004.9
V. hederifolia	584	384	46.5
V. persica	1894	936	350.2
V. arvensis	1007	233	159.4

Effects of nitrogen fertiliser on weed seed production

In all years, seed production of *A. fatua* and *G. aparine* increased as the level of nitrogen increased (Table 7). These increases were three times larger in 1990 and almost double in 1991 and 1992 at the highest nitrogen level compared with no nitrogen. Other species showed no response to nitrogen.

Table 7. Effect of nitrogen on the number of seeds per plant (1992 data, mean of two crop densities)

Species		Nitrogen kg/ha 0	50	100	200	s.e.d.
A. fatua	1990	416	692	808	1469	174.2
	1991	530	869	1367	1017	239.2
	1992	720	917	1169	1100	261.1
G. aparine	1990	65	95	149	241	61.7
	1991	273	329	359	534	61.0
P. rhoeas	1992	46002	41429	55769	43279	12770.3
T. inodorum	1992	5246	4871	5693	5175	2400.6
V. hederifolia	1992	489	463	528	457	47.0
V. persica	1992	1159	1315	1597	1590	547.1
V. arvensis	1992	455	786	569	669	203.9

DISCUSSION

Results of the various techniques of seed determination showed good agreement between years for weed species studied in more than one experiment. For *A. fatua* and *P. rhoeas*, numbers of seeds/g fresh weight of panicle and capsule were similar between the three years, and seed numbers of *L. purpureum* showed good agreement for both years. *V. arvensis* was less consistent from year to year; numbers of seeds per capsule in 1988 and 1989 agreed with the findings of Doohan *et al.* (1992) (45-50 seeds/ capsule), but were lower in 1992, similar to the data of Franz *et al.* (1990) (30 seeds/capsule).

Strong evidence of linear relationships was found between estimated seed production and plant dry weight for all species. These relationships were similar between years for *A. fatua, G. aparine* and *P. rhoeas*. Although weed biomass was affected by season, the seed/biomass relationship was more stable between years, and may be used to model seed production for most species. These relationships may not apply to herbicide-treated weeds, as Pedersen & Rasmussen (1990) have previously shown a larger reduction of seed production than that of plant biomass for several species of herbicide- treated weeds. However, later work (Rasmussen, 1993) suggested that herbicides may not always affect the seed number/biomass relationship.

The present results confirm the strong influence of crop competition in limiting seed production in weeds. With all the weed species studied, seed production was reduced as crop density increased. Even very low wheat densities (40-45 plants/m^2) reduced seed production by 85-95% compared with weeds grown in the absence of crop. Seed production of two of the most competitive weeds, *A. fatua* and *G. aparine* (Wilson & Wright 1990), increased as the amount of added nitrogen fertiliser was increased, confirming previous work by Thurston (1959) and Franz *et al.* (1990).

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SEED PRODUCTION OF A MIXTURE OF TWO *POLYGONUM* SPECIES AT NORMAL TO VERY LOW HERBICIDE DOSES

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ABSTRACT

Polygonum species (*P. persicaria* and *P. lapathifolium*) were sown into spring barley crops in 1990 and 1991 and sprayed with different herbicides at approved and reduced doses. Seed production was reduced significantly at doses as low as 1/32 of the approved dose. The reduction of seed production necessary to avoid enlarging the soil seed reserve is calculated by a model to be between 15 and 85%, depending on model assumptions.

INTRODUCTION

A build-up of seed reserves in the soil is of growing concern to farmers who are forced to minimize the use of herbicides. In Denmark, the required reduction in use of herbicides is mainly achieved by using lower doses of herbicides (Kudsk, 1989). Since 1989 research has been carried out to determine the effects of reduced herbicide doses on the seed production of target weeds, part of this research has concerned *Polygonum persicaria* and *Polygonum lapathifolium* in spring barley. The response of seed production to herbicide doses is crucial to establish the minimum dose required to keep the soil seed reserve at equilibrium. A model describing the changes in the soil seed reserve is applied to determine the minimum dose required to keep the soil seed reserve at equilibrium.

METHODS

Experiments

Two field experiments were conducted, one in 1990 and one in 1991, on a loamy soil at Flakkebjerg, Denmark. A spring barley crop of approximately 400 plants m^{-2} was established (by sowing 150 kg ha^{-1}) and at the same time fertilizer was applied (84 kg N ha^{-1}, 16 kg P ha^{-1} and 40 kg K ha^{-1}). A population of approximately 400 plants m^{-2} of *Polygonum persicaria* and *Polygonum lapathifolium* was established by sowing a mixture of their seeds a few days later with a crop-seeder without the tubes connected, the seeds were worked into the soil by the finger-tines behind the seeder. Five herbicides and maximum rates of application were chosen to control *P. persicaria* and *P. lapathifolium* (Baandrup & Ballegaard, 1989). Four of the herbicides were used in 1990, at 6 doses each, with the maximum dose the same or greater than the approved dose; the lowest rate was 1/32 of the maximum. Three of the herbicides were used in 1991, at 5 doses each. The herbicides used and the maximum and approved doses are shown in Table 1.

TABLE 1. Active ingredients and maximum (Max.) and approved (App.) doses of herbicides used to control *Polygonum* species.

Herbicide code	Active ingredients	Dose (g ha^{-1})	
		Max.	App.
1	Tribenuron 75% + 0.05% non-ionic surfactant (Extravon)	10	10
2	Bromoxynil 200 g/l + Ioxynil 200 g/l	800	800
3	Dichlorprop 667 g/l	2335	2000
4	Dichlorprop 534 g/l + MCPA 133 g/l	2000	2000
5	Bromoxynil 23 g/l + Ioxynil 38 g/l + Dichlorprop 184 g/l + MCPA 235 g/l	1440	1200

Treatments were arranged in randomized blocks with four replicates with unsprayed plots in each block equal to the number of herbicides. Herbicides were applied to plots (2.5 by 2.5 m) with a plot-sprayer in a volume of 150 l ha^{-1}. Herbicides were applied when the barley was at GS 21-23 (Tottman, 1987) and the *Polygonum* species had 2-4 expanded true leaves in 1990 and 1-2 expanded true leaves in 1991. *Polygonum* plants were counted in untreated plots shortly after the time of spraying. Five to six weeks after spraying, *Polygonum* plants in 0.5 m^2 quadrats were cut off at the soil surface, dried and weighed.

At the beginning of seed shedding, four flat aluminum-foil trays with drainage holes and half filled with fine sand were placed on the soil surface in each plot to collect the weed seeds. In 1990, trays were placed in all plots and in 1991, only in the untreated plots. When barley was close to maturity, weeds were harvested from 0.5 m^2 (1990) or 1 m^2 (1991) quadrats. Plants were counted, dried at 35°C, weighed and threshed; seeds were cleaned, weighed and counted. After seed harvest, the trays were collected, the sand sieved away and the seeds counted.

Data analysis

Total seed production was calculated by adding the average seed shed m^{-2} to the seed harvested m^{-2}. Total seed production and number of seeds harvested were linearly related (r^2 = 0.89). Because of this close relationship, seed shed was measured in untreated control plots only in 1991, and results for harvested seed have been used for calculations both years. Relative seed production at the different doses of each herbicide was calculated as the proportion of the weed seeds harvested in the control plots. Relative seed production was compared with untreated controls by analysis of variance (SAS Institute, 1985) and significant differences established.

Seed balance model

The level of seed production that can be allowed without enlarging the soil seed reserve is calculated from the equation based on work by Holzmann & Niemann (1988) and Zwerger & Hurle (1988 & 1990):

$$S_{t+1} = S_t * s_c + S_t * g * (1\text{-}m) * p * (1\text{-}r) * s_h * s_b$$

where

S_{t+1} = soil seed reserve before following growing season (seed m^{-2})
S_t = soil seed reserve before first growing season (seed m^{-2})
s_c = proportion of the old seed reserve that survives from before the first growing season to before the following growing season
g = proportion of the soil seed reserve that germinates
m = proportion of plants that do not survive from germination to maturity
p = seed production $plant^{-1}$
r = reduction in total seed production caused by herbicide use
s_h = proportion of new seeds that survive until incorporation into the soil
s_b = proportion of new seeds in the soil that survive between growing seasons.

The aim is to find the level of control (the reduction in seed production caused by herbicide use, **r**) needed to maintain the soil seed reserve at equilibrium, thus $S_{t+1} = S_t$. The product of the (theoretical) soil seed reserve (S_t), the germination rate (**g**) and one minus the mortality rate (**m**) equal the plant number. This value, as well as the value for seed production (the product of plant number and seed production $plant^{-1}$ (**p**)) are supplied from the results of the experiments. The model does not take account of different seed production $plant^{-1}$ and different mortality as influenced by plant number or competition from crop or other weeds. Values for the proportion of the soil seed reserve that germinates (**g**), the proportion of seeds that survive until incorporation into the soil (s_h) and the proportion of seeds in the soil reserve surviving until the next growing season (s_c and s_b) need to be provided. A range of values was established based on published estimates from "best case", where the combination of these proportions makes the needed level of control small, to "worst case", where the combination of these proportions makes the needed level of control great. The proportion of the soil seed reserve that germinates (**g**) at the start of the growing season has been established for a mixed population of broad-leaved weeds to between 0.5 and 8 % by Hurle *et al.* (1988), and between 3 and 6 % by Roberts and Ricketts (1979). Values between 2 and 10 % have been used in the calculations, only values between 5 and 7.5 % are shown here. The proportion of seeds that

TABLE 2. Combinations of values of parameters used in model. Each case corresponds to a level of necessary reduction shown in Fig. 3 and 4.

Case	**g** germination rate	s_c survival rate entire cycle	s_h survival rate harvest	s_b survival rate between seasons
1	5 %	50 %	75 %	50 %
2	5 %	50 %	50 %	90 %
3	5 %	50 %	75 %	90 %
4	7.5 %	50 %	75 %	90 %
5	7.5 %	75 %	75 %	75 %
6	7.5 %	75 %	75 %	90 %

survive from production until incorporation into the soil seed reserve (s_b) might be between 10 and 90 %(Sagar & Mortimer 1976), for the model values between 25 and 75 % have been used, only values between 50 and 75% are shown. Roberts and Feast (1973) state that the proportion of the soil seed reserve of a mixed weed population that is lost during the year ($1-s_c$) is between 30 and 60 %. In the model the values used for s_c have been between 25 and 75 %, since the *Polygonums* are known to be long-lived (Milberg 1990), results are shown for 50 and 75%. The loss from incorporation into the soil until the start of the next growing season ($1 - s_b$) is less than the loss over a whole year, particularly in the case of winter crops. The rates of loss might also be different for the same period of time for the new seed input and the old seed reserve. For the calculations, values between 25 and 90 % have been used, examples show values between 50 and 90 %. Six combinations of values are shown (Table 2), "best cases" where some of the parameters are at low values, and "worst cases" where some or all of the parameters are at their maximum.

RESULTS

Maximum dose of the herbicides gave complete control of seed production (Fig. 1 and 2). Control declined as dilution increased. The number of seeds produced was decreased by all herbicides in both years at doses as small as 1/32 of the maximum dose.

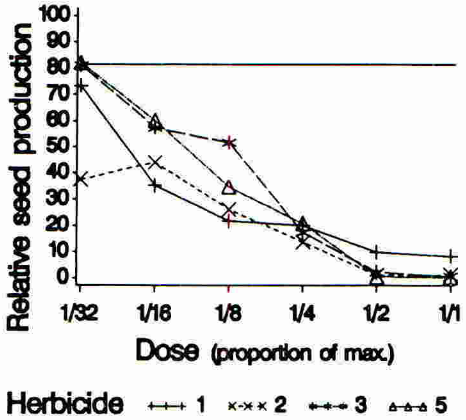

FIGURE 1. Reduction in seed production due to herbicide treatment relative to untreated control 1990. 100 = 3789 seeds m^{-2}. Results below the solid line are significantly different from control at $p \leq .05$.

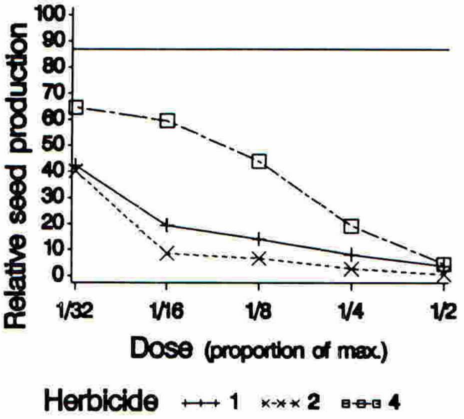

FIGURE 2. Reduction in seed production due to herbicide treatment relative to untreated control 1991. 100 = 1244 seeds m^{-2}. Results below the solid line are significantly different from control at $p \leq .05$.

The level of control needed to keep the soil seed reserve at equilibrium in the two experiments was modelled and the different assumptions led to different requirements for efficacy of control (Fig. 3 and 4). The differences between years are caused by different population sizes and subsequent different seed production. The largest level of control needed was found in situation 6, 1990, where a reduction in seed production of 85% was necessary to keep the soil seed reserve at an equilibrium.

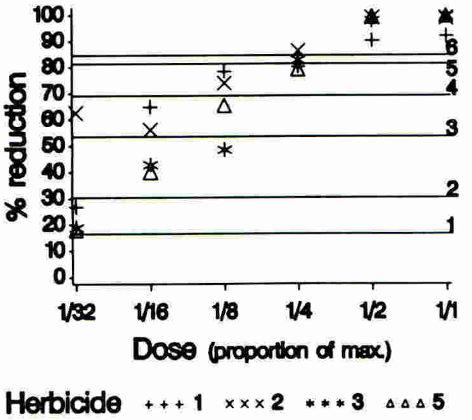

FIGURE 3. Reduction in seed production as percent of control 1990. Lines represent the levels of the 6 cases of control needed in Table 2.

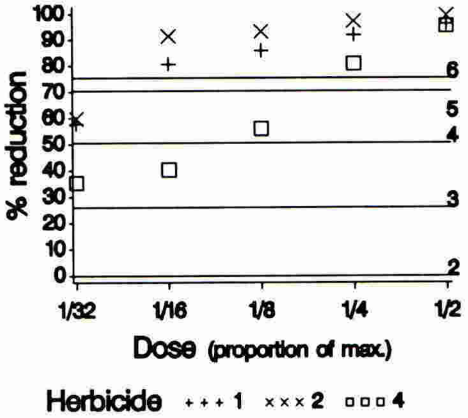

FIGURE 4. Reduction in seed production as percent of control 1991. Lines represent the levels of the 6 cases of control needed in Table 2 - case 1 fell below 0 % reduction needed.

DISCUSSION

It is known that reduced doses of relevant herbicides can control weeds in well-established cereals without significant loss of yield (Kudsk, 1989). The question is whether it is possible to maintain a reasonable weed population in the future, or whether weed seed production with less than full insurance use of herbicides will result in increasing populations (Lawson *et al.*, 1992). Rasmussen (1993) has found that even 1/8 of the normal dose of some herbicides has been sufficient to avoid enlarging the soil seed reserve of *Chenopodium album*. This paper shows that the seed production in these experiments were significantly lower than untreated controls at 1/32 of the approved dose. But is this enough? There are many variables influencing the size of the seed bank. Nevertheless, the attempt here has been to identify the minimum efficacy of control necessary given certain assumptions on the seed bank. The model used suggests that with the "worst case" assumptions, a reduction of seed production of 85% is necessary, while with the "best case" assumptions, 15% reduction of seed production is sufficient to avoid increasing the soil seed reserve. The requirements are likely to fall between those two extreme values in most cases. The reduction in seed production brought about by reduced herbicide doses might well be sufficient to avoid enlarging the soil seed reserve, 1/2 to 1/16 of the maximum dose has been enough to reduce the seed production as much as needed in the "worst case".

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BRIGHTON CROP PROTECTION CONFERENCE - Weeds - 1993

MORPHOLOGICAL AND PHYSIOLOGICAL VARIATION IN WILD OAT

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ABSTRACT

Wild oat (Avena ludoviciana Dur.) grows and persists under a wide range of climatic and edaphic conditions in Greece. The present study was conducted to examine the variation of wild oat populations collected from cereal fields in Greece in terms of morphology, dormancy and herbicide responses. Research was carried out in pots or in spaced plant trials in the field. The wild oat accessions differed in leaf length and width, heading date, plant height, number of panicles per plant, panicle length, spikelets per panicle, seed weight and response to herbicides. Seed dormancy varied between accessions. Seeds from different populations showed different patterns of emergence over 19 months when compared under the same conditions.

INTRODUCTION

Wild oat (usually Avena ludoviciana but very occasionally A. fatua) is the most common and troublesome weed in the main winter cereal areas in Greece where it is well adapted to grow and persist under a wide range of climatic and edaphic conditions. This wide distribution might indicate considerable genetic diversity in the populations.

Several reports have indicated variation in wild oat based upon plant morphological characteristics (Thurston, 1957; Miller et al.; 1982, Somody et al.; 1984, Thurston, 1957) and dormancy (Peters, 1991). There are few reports from Greece on concerning A. ludoviciana. Toole and Coffman (1940) indicated that dormancy was not related to plant morphological characteristics.

Studies have indicated significant amounts of inter -and intra-population variability in reaction to herbicides. Wild oat samples also have been reported to differ in susceptibility of herbicides (Miller et al., 1982; Somedy et al., 1984) Differences in susceptibility of wild oat to some herbicides was not related to seed colour, lemma pubescence, or callus pubescence (Jacobsohn and Andersen, 1968; Rydrych and Seely, 1964). Further studies showed that leaf area, flowering time and height were not different in untreated conditions but leaf area was lower in the case of diclofop-methyl resistance (Olufunmilayo et al., 1990). Populations which had a long history exposure to herbicide had significantly higher frequencies of tolerant plants (Jana and Naylor, 1982; Thai et al., 1985).

The objectives of these experiments were: a) to determine variation in morphological and physiological characteristics of Avena ludoviciana accessions from various areas of Greece and b) to determine variation in susceptibility of the same accessions to diclofop-methyl and imazamethabenz herbicides.

MATERIALS AND METHODS

More than one hundred accessions of wild oat collected from the main cereal areas of Greece were used in this research. In all cases individual accessions were gathered either as a single panicle or a single plant. Only three accessions were A. fatua and the rest were A. ludoviciana. Wild oat accessions were evaluated in the field. The soil was silty-clay with pH 7.4. In the season prior to the experiment the field was free of wild oat plants.

Growth characteristic

Primary seeds from spikelets with uniform size were selected and sown in the field on November 15, 1990. Fifty seeds of each accession were placed in each of two rows spaced 50 cm apart. Plants were thinned to five per row 25 cm apart at the two leaf stage. The experiment was a randomized complete block design with four replicates. Type of first growth (erect, semi-erect and prostrate), height of plants, heading day (first panicle emergence after 1st February), number of panicles per plant and length of panicles, number of spikelets per panicle and seed weight were determined at maturity. Also the main second leaf blade length from the ligule to the tip and maxumum width, were determined.

Herbicide response

Seed from populations of wild oat which had been grown for seed production during 1991-1992 were sown in the field on 23 December in two rows 1.5 m long and 30 cm apart for each population, with 50 seeds per row. There was a one row gap in between populations. The experiment had four replicates with herbicides as main plots and populations as subplots. After germination the plants were thinned to ten plants per row.

Imazamethabenz was applied at 600 g AI/ha and Diclofop-methyl 900 g AI/ha at the tillering stage. Treatments were applied using a plot sprayer with a 2 m boom and spray volume range 300-400 l/ha in April 1993. Two and three weeks after spraying the plants were assessed using the visual assesment score 0-9, where 0=no effect and 9=completely killed.

Germination test

Four hundred primary seeds from each population were sown at a depth of 25 mm in soil in four plastic pots (150 mm in diameter, 50 mm deep) filled with a sandy loam soil. The pots were placed in the field and were kept moist by watering. The number of germinated plants was recorded weekly and the emerged seedlings removed. The soil was disturbed periodically. Seedling emergence ceased after 19 months. For analysis, seedling emergence was examined in four periods. October to December 1991. January to June 1992, October to December 1992 and January to April 1993. Analyses of variance were performed and when the treatment effect was significant the treatment means were compared using LSDs.

RESULTS

Morphological Variation

The wild oat accessions grown in the field varied significantly in all morphological attributes assessed. From 115 accessions only three had

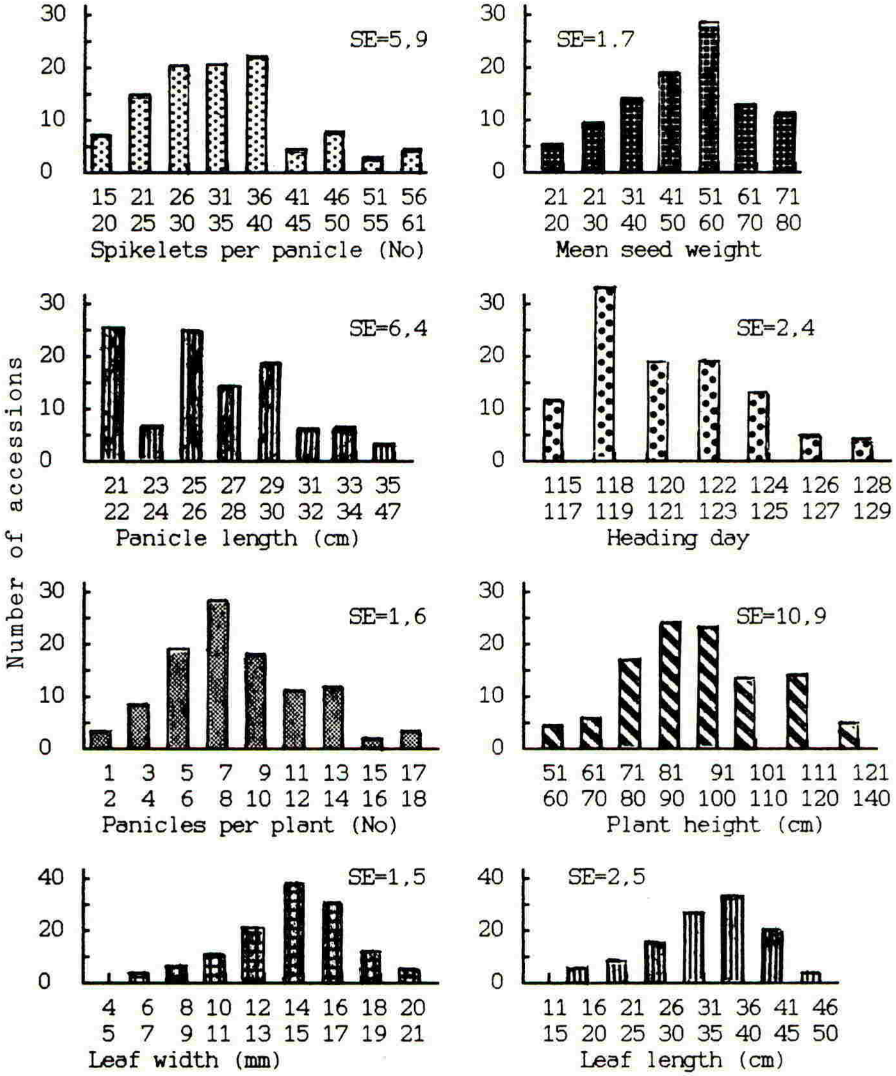

FIGURE 1.Leaf width and length, plant height, days to emergence panicles per plant, length and spikelets per panicle of wild-oat accessions.

prostrate growth during winter. The three populations of A. fatua had erect growth. Differences in leaf length and width (Fig. 1) were highly significant and ranged very widely. Different in plant height of wild oat accessions, days to panicle emergence, length of panicle, panicles per plant, spikelet number per panicle and 1000 seed weight were highly significant and ranged very widely and tending to have a normal distribution for each parameter exept for panicle length. The accessions with the heaviest seeds were not those with the largest seed (data not shown), whilst others were the tallest plants.

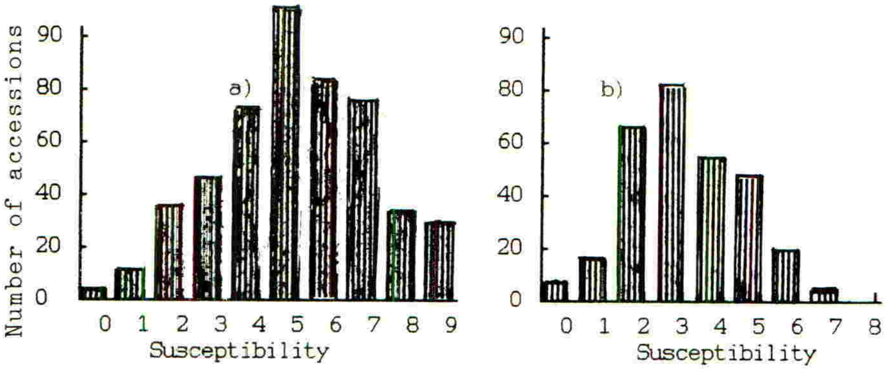

FIGURE 2. Control of wild oat accessions with a) Imazamethabenz and b) diclofop

Herbicide Response

A. ludoviciana accessions varied widely in response to diclofop and imazamethabenz both between and within populations (Fig. 2). Generally accessions were less susceptible to diclofop compared to imazamethabenz. Those wild oat accessions resistant to diclofop were controlled effectively by imazamethabenz. Some populations were very susceptible to imazamethabenz and also moderately susceptible to diclofop. Imazamethabenz usually caused a reddening of wild oat leaves two weeks following spraying but in some accessions subsequent growth was without symptoms but was less vigorous than the control.

Germination

At the end of experiment, not all ungerminated seed was retrieved. Thus these results have to be treated with caution.

Seedling emergence was related to soil temperature and rainfall. Some emergence occured ten days after sowing in October 1991. At this time and for the rest of the winter and spring, emergence was not limited by soil moisture. The seeds that did not germinate in October experienced warm (5-17° C), moist conditions until the begining of November, and then a period of chilling below a mean 4°C. After the chilling period the temperature rose above 4°C at the end of January and emergence then recommeneded being greatest in February and March. At the begining of October 1992 there was a small flush of emergence.

The proportion of seed that was dormant and the time required for seeds to lose dormancy differed considerably between accessions (Fig. 3). Accessions also differed significantly in median germination time (time to 50% final germination).

DISCUSSION

Wild oat populations differed significantly from each other in terms of one or more characteristics. Intraspecific variation in almost all characters has been shown for many species including wild oat (*A. fatua*) (Miller *et al*., 1982; Peters, 1991) and the variation shown here gaves a measure of the genetic variation between populations of *A. ludoviciana* occurring in Greece. Indivicual characters might be interpreted as conferring advantages or reflecting selection in particular enviroments. Earlier flowering might permit higher fecundity if panicle production continues and might result in increased seed output. Larger seed size providing greater nutritional reserves might permit faster seedling establishment or greater seed lorgevity. Prostrate or erect growth during winter influences the degree of frost injury.

The protracted dormancy of some accessions might allow avoidance of the detrimental effects of autumn cultivation, whereas for populations with rapid germination and establishment would be disadvantaged. It is likely that cultural practices have selected for seed dormancy and delayed germination within populations enabling the formation of a persestent seedbank. The large differences in the level of dormancy between populations is of considerable relevance to models of population dynamics of *A. ludoviciana* which need to take into account such differences to be realistic.

Emergence in winter/spring was associated with periods of increasing temperature immediately following chilling. No further emergence from any population occurred in July to September when temperatures were very high. Lack of emergence in autumn 1992 for some populations was probably due to only few viable seeds remaining at that stage.

Provided water is not a limiting factor, the present evidence suggests that flushes of *A. ludoviciana* emergence during the winter/spring can be predicted by monitoring soil temperature. When the soil temperature falls bellow the chilling temperature of 4°C, emergence is likely in a following warm period.

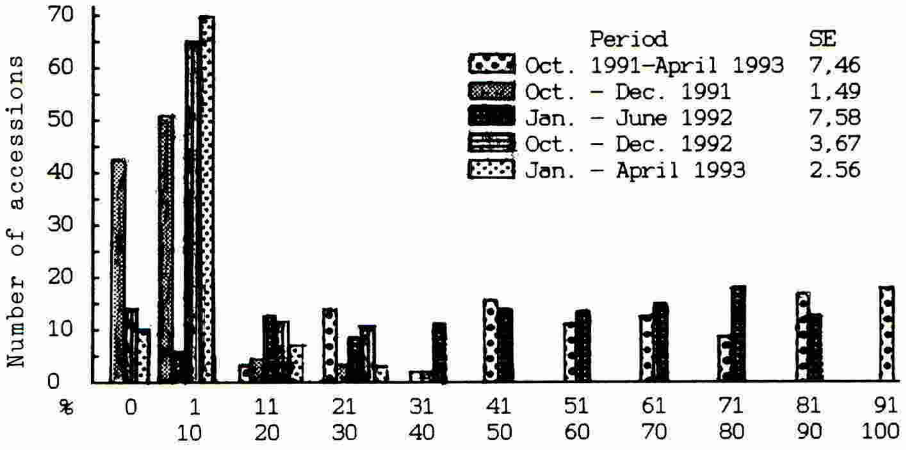

FIGURE 3. Percent emergence of wild oat accessions grown in Thessaloniki from October 1991 to April 1993.

Significant differences were found between the populations with response to two herbicides. The response of A. ludoviciana populations to herbicides appears to be genetically determined. Diclofop has been used since 1977 in winter cereals in Greece, whilst imazamethabenz had not been used before the collection of seed for this investigation. Succeptibility is higher to imazamethabenz than to diclofop. This could be taken as evidence for increased tolerance of some populations resulting from selection pressure to this herbicide Diclofop has been used since 1977 in winter cereals in Greece, whilst imazamethabenz had not been used before the collection of for this investigation. However, the range of susceptibility to imazamethabenz indicates that increased tolerance to herbicides is not dependent on previous history of herbicide use. The presence of tolerant phenotypes in wild oat populations never exposed to imazamethabenz raised the possibility of natural selection favouring the corresponding resistance genes. It is noteworthy that the least susceptible populations were from intensively farmed arable fields.

Further studies of these populations will be needed before reliable predictions of emergence and herbicide response can be made. Current investigations are continuing to determine whether the origin of seed production influences the germination pattern of these populations and their herbicide response.

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PATTERNS OF ABUNDANCE IN THE WEED SEED BANK

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ABSTRACT

The patterns of abundance of weed seeds in the seed bank of a cultivated field at the University of East Anglia, Norwich were investigated after a two-year ley. Three hundred and twenty five soil cores were taken in a 2.5 x 14 m area and the composition and size of the seed bank were estimated by monitoring seedling emergence from the cores. While two thirds of the species were annuals, the seed bank was dominated by *Epilobium tetragonum* and *Agrostis stolonifera*; the most common annual was Senecio vulgaris. The pattern of species abundance did not fit either the geometric series, the broken-stick model, the logarithmic series or the lognormal distribution. Most of the seeds were patchily distributed. The relationship between the variability in the abundance of seeds and average seed density conformed to a simple power law. While the rank order of abundance of seeds was significantly correlated with that of seedlings following cultivation, the two most common species in the seed bank were under-represented amongst the seedling flora.

INTRODUCTION

The seed banks in cultivated soils, which are an accumulation of the weed seeds buried in the soil and on the soil surface, are derived from seeds produced in the area and those that have dispersed in from elsewhere. Numerous studies (see Roberts, 1981; Cavers & Benoit, 1989) have been carried out to investigate the composition and size of the seed banks in cultivated fields. The vast majority of seeds entering the seed bank come from annual weeds growing on that land (Roberts, 1981) and consequently the seed bank is dominated by annual species. The size of the seed bank has been shown to vary from 250 to 46819 seeds m^{-2} in vegetable crops and from 4742-73350 seeds m^{-2} in small grain cereal crops (Cavers & Benoit, 1989). Many of the higher estimates come from data collected before herbicides came into general use. Apart from herbicides it is known that cropping regime, soil type, cultivation, fertilizers and manures all affect the numbers of seeds and the composition of the weed seed bank in arable land.

Typically most species in the seed bank are represented by relatively few seeds while the bulk of the seeds are derived from only a few species (Chauvel *et al.*, 1989). There have however been few attempts to quantify the relative pattern of abundance of species in the seed bank. It has been suggested (Dessaint *et al.*, 1991) that the type of spatial pattern shown by species in the seed bank is dependent upon their abundance with the higher density species showing a more aggregated pattern than the low density species which tend to have a random pattern. In particular it has been suggested that the index of mean crowding (Lloyd 1967) increases linearly with mean abundance in the seed bank (Dessaint *et al.*, 1991). In this paper, we examine this hypothesis and quantify the size and composition of a seed bank in cultivated soil and relate the spatial pattern of seeds to their abundance in the seed bank (Roberts, 1981).

MATERIALS AND METHODS

Site and experimental procedure

The study was carried out at the Experimental Field of the University of East Anglia, Norwich. The field is used for carrying out agricultural experiments and had previously been planted with wheat, carrots and peas. For experimental purposes, the field was planted with

Agrostis stolonifera in 1990 for two years before being rotavated in early April 1992. The soil is a sandy loam.

The seed bank analysis was carried out in an area of 35 m^2 (14 X 2.5m) in the field that was to be used for horticultural crops. Soil cores were taken from random positions throughout the sampling area on 15 April 1992. A sample of 325 soil cores (4.7 cm diameter and 15 cm deep) was collected. These were air-dried for ten days and sifted to eliminate stones. A thin layer of each soil core was then spread on the top of Levington Multi-purpose Compost in seed trays 20 x 15 cm in area and 5 cm in depth. In total three hundred and fifty seed trays were prepared, twenty-five of which contained only the compost and were used as controls. The trays were watered to keep the soil moist and the soil was disturbed at regular intervals. The trays were arranged randomly on unheated greenhouse benches, and their positions were frequently re-arranged. Emerging seedlings were counted and identified (Stace, 1991) and removed at two-week intervals for the first three months. After that counts were made at one-month intervals. Unidentifiable seedlings were transplanted into small pots until they could be identified.

The plot was planted in the spring with cabbages, sprouts, beetroot, carrots, beans and leeks. The number of seedlings emerging in the field following cultivation and planting was estimated from April to August by counting the number of seedlings that appeared in thirty 40 x 50 cm permanent quadrats that were positioned at random over the plot.

Analytical methods

Species-abundance relationship

A number of models have been proposed to describe the species-abundance relationships in biological communities (Gray, 1987). Here we fit four of the more commonly used models to the data: the geometric series, the broken-stick model, the logarithmic series and the lognormal distribution (May, 1975). The goodness of fit of each of the models was tested using the Chi-square test.

Spatial pattern

Various measures have been employed to analyse the spatial patterns of individuals in biological communities (Greig-Smith, 1983). In this study we quantify the mean number of seeds per core (*m*), the variance in the number of seeds (*V*) and the index of mean crowding (m*):

$$m^* = \sum_{i=1}^{n} x_i(x_i - 1) \;/\; \sum_{i=1}^{n} x_i$$

(Lloyd, 1967) for each species. The variance: mean ratio was tested to see if it was significantly different from unity; values greater than unity indicate an aggregated or patchy distribution of seeds. Values of $m^* > m$ indicate aggregated distributions.

RESULTS

The seed bank consisted of 45 species (Fig.1) which were primarily annual (69%) or short-lived perennial species, most of which were represented by low densities of seeds. The seed bank was dominated by *Epilobium tetragonum*, *Agrostis stolonifera* and *Senecio vulgaris*, which represented 31%, 23% and 7% of the seed bank, respectively. The frequencies of their occurrence in the sample were 84%, 83%, and 44%, respectively. A second subset of 11 species, *Arabidopsis thaliana, Betula pendula, Capsella bursa-pastoris, Chenopodium album, Erigeron canadensis, Poa annua, Stellaria media, Papaver rhoeas, Polygonum aviculare, Urtica urens* and *Veronica agrestis* contributed another 29%. The remaining 10% were shared among the other 31 species.

Species-abundance relationships

The relative abundance of the 45 species in the seed bank is illustrated in Fig.1. Neither the geometric series, the broken-stick model, the logarithmic series or the lognormal model provided a significant fit to the data. The broken-stick model provided an extremely poor fit to the data. In comparison with the geometric series the most abundant species in this data set were too common whereas there were too few species represented by a few individuals to provide a good fit to either the lognormal distribution or the logarithmic series.

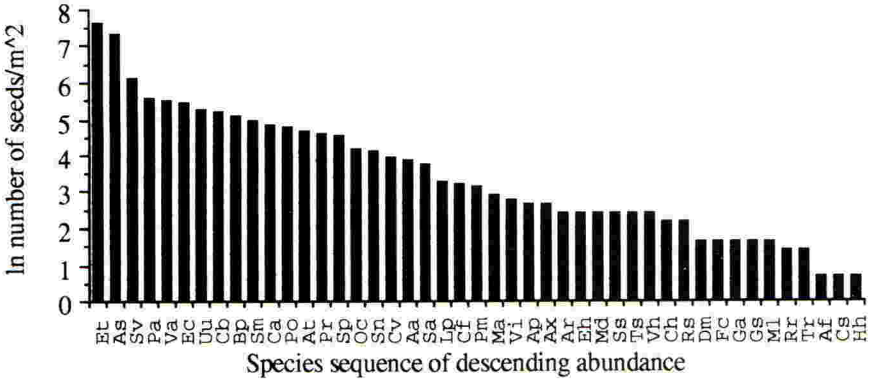

Fig.1 Relative abundance of the seed bank of the forty-five species. Ranks are: Et *(Epilobium tetragonum);* As *(Agrostis stolonifera);* Sv *(Senecio vulgaris);* Pa *(Poa annua);* Va *(Veronica agrestis);* Ec *(Erigeron canadensis);* Uu *(Urtica urens);* Cb *(Capsella bursa-pastoris);* Bp *(Betula pendula);* Sm *(Stellaria media);* Ca *(Chenopodium album);* Po *(Polygonum aviculare);* At *(Arabidopsis thaliana);* Pr *(Papaver rhoeas);* Sp *(Sagina procumbens);* Oc *(Oxalis corniculata);* Sn *(Salonum nigrum);* Cv *(Cirsium vulgare);* Aa *(Anagallis arvensis);* Sa *(Sonchus arvensis);* Lp *(Lamium purpureum);* Cf *(Cerastium fontanum);* Pm *(Persicaria maculosa);* Ma *(Mercurialis annua);* Vi *(Viola arvensis);* Ap *(Aphanes arvensis agg.);* Ax *(Atriplex patula);* Ar *(Arenaria serpyllifolia);* Eh *(Epilobium hirstum);* Md *(Matricaria discoides);* Ss *(Salix sp.);* Ts *(Taraxacum sp.);* Vh *(Veronica hederifolia);* Ch *(Cardamine hirsuta);* Rs *(Rumex sp.);* Dm *(Diplotaxis muralis);* Fc *(Fallopia convolvulus);* Ga *(Galium aparine);* Gs *(Geranium sp);* Ml *(Medicago lupulina);* Rr *(Raphanus raphanistrum);* Tr *(Trifolium repens);* Af *(Avena fatua);* Cs *(Chenopodium sp.);* Hh *(Hedera helix).*

For those species with more than 40 seeds per square metre in the seed bank in April there was a significant rank correlation with seedling abundance in the subsequent growing season from April to August ($r_s = 0.522$, $n = 20$, $p < 0.05$); a linear correlation provided a very poor fit to the data ($r^2 = 0.01$, $n = 20$, ns). *Agrostis stolonifera* and *Epilobium tetragonum*, the two most abundant species in the seed bank were, however, significantly under represented in the seedling flora. The exclusion of these two species from the analysis resulted in a significant linear correlation between the number of seedlings and the number of seeds ($y = 0.99x - 27.83$, $r^2 = 0.561$, $n = 18$, $p < 0.001$).

Spatial pattern

The analysis of spatial pattern in the seed bank was restricted to those species which had more than 0.1 seeds per core. For 16 of these 17 species the variance:mean ratio was significantly greater than unity ($p < .05$) indicating that the seeds were aggregated. With the exception of *Papaver rhoeas* all of the other species were above a line of slope equal to unity when the index of mean crowding was plotted against the mean number of seeds per core (Fig.2). This again indicates an aggregated spatial pattern. The index of mean crowding increased with the number of seeds per core ($m^* = 1.41m + 1.79$, $r^2 = 0.27$, $n = 17$, $p < 0.05$) although the relation only accounted for 27% of the variance in the data.

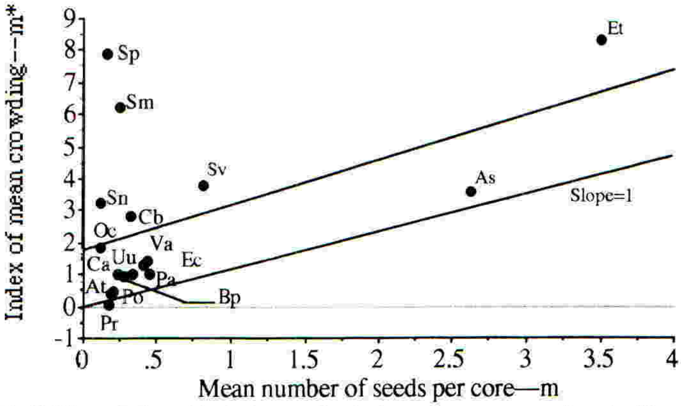

Fig.2 The relationship between the index of mean crowding (m^*) and the mean number of seeds per core (m) for the 17 species with more than an average of 0.1 seeds per core. See Fig.1 for species codes.

DISCUSSION

Composition and size of the seed bank

There were 45 species of weeds present in the seed bank studied and a total density of seeds of 6502 per square meter in the top 15 cm of soil. The numbers of species and size of the seed bank are not dissimilar to these reported elsewhere (e.g. Chauvel *et al.*, 1989). The abundance of *A. stolonifera* in the seed bank reflects the fact that the plot had been sown to a grass ley of *A. stolonifera* in the previous two years while that of *E. tetragonum* may reflect the irregular cropping pattern. While many of the seeds in arable soils come from plants growing on that land it is clear from the presence of a number of species such as *B. pendula* and *H. helix* that a number of species were dispersed into the plot from a nearby (40 m) woodland margin.

Typically the seedlings that emerge following cultivation account for only a low percentage of the viable seeds present in the soil (Roberts, 1981). In our study a high proportion (39%) of the seeds would appear to have emerged following cultivation. It is not clear to what extent this is a true reflection of the abundance of seeds in the seed bank. For *E. canadensis* and *U. urens* it would appear that the seed bank analysis underestimated the number of seeds. It is however also possible that seeds of the former had dispersed into the area from outside the plot and that newly produced seeds of the latter had produced seedlings during the intervening period.

Although many of the dominant species in the seedling flora were well represented in the seed bank, the two most abundant species in the seed bank, *A. stolonifera* and *E. tetragonum* were significantly under-represented. Many species show distinct patterns in the seasonal distribution of seedling emergence (Roberts, 1981) and the species composition of the seedling population is likely to be influenced by the time at which the soil is disturbed. A flush of seedlings of both *A. stolonifera* (131) and in particular *E. tetragonum* (3655) occurred in the month prior to cultivation. Consequently the early spring germination of these two species may account for why they were poorly represented in the seedling flora after cultivation. Amongst the remaining species there was a strong linear correlation between the number of seeds and the subsequent number of seedlings.

Species-abundance relationship

Most relative abundance distributions are drawn up with data on mature plants. The structure of such distributions, however, reflects the outcome of a series of population dynamics processes: seed dispersal, seed dormancy, seed germination, establishment, growth and mortality. Therefore, the distribution of the relative abundance of species in a community fluctuates during the course of community development. For weed communities, it might be expected that there would be considerable fluctuations in relative abundance over time due to irregular disturbance. The dominant species in the community can be expected to be those which have recently enjoyed a large *r* and/or those with a persistent seed bank. It has been suggested (May, 1975) that the lognormal distribution may be expected to represent an assemblage of opportunists, but it has also been suggested that 'equilibrium' communities usually fit the lognormal distribution. Similar problems have arisen in the interpretation of the biological meaning of fits to the logarithmic series distribution (Gray, 1987). Empirical data suggest that early successional communities generally fit the geometric series while, as more species appear, the community develops through a log series or lognormal model before perhaps returning to a geometric series at the climax (Gray, 1987).

The pattern of species abundance in the seed bank showed that a few species dominated the seed bank and that most species were relatively uncommon. None of the four models however provided an adequate description of the pattern of abundance. Further studies of the patterns of abundance in weed seed banks are required, however, before generalizations can be made of the significance of this result. The pattern of abundance in an arable seed bank is clearly dependent upon those species which have recently enjoyed a large *r* but the cropping history and pattern of disturbance together with the longevity of seeds in the soil can all be expected to influence relative abundance.

Spatial pattern

A range of studies have demonstrated that the spatial pattern of weed seeds in the soil is typically aggregated (Bigwood & Inouye, 1988; Chauvel *et al.*, 1989; Dessaint *et al.*, 1991). Our results confirm this generalisation. The spatial pattern of seeds will be determined by the interplay between the distribution of parent plants producing seeds, the pattern of the seed rain about each parent plant and the abundance and foraging behaviour of granivores. Clearly the pattern of agricultural activities can subsequently be expected to modify the original spatial distribution of seeds.

For single species populations of varying densities it has been shown that the degree of aggregation in the population can be related to the mean density of individuals (Iwao 1968). Iwao related the index of mean crowding (Lloyd, 1967), m^*, to the mean density of populatons, m, using the linear equation: $m^* = a + b\,m$ (where a and b are fitted parameters and b can be considered to represent a mean aggregation index). Bigwood & Inouye (1988) have applied this method to optimizing sampling from soil seed banks while Dessaint *et al.* (1991) have applied the method to a comparison of the pattern of aggregation in different species. They found that 97% of the variation in m^* for a range of species could be explained by a linear regression on m. In our study only 27% of the variation in m^* could be explained by changes in mean density (Fig.2). The applicability of the m^*-m relation to community data clearly requires further evaluation.

An alternative model to relate the mean and variability of spatially distributed populations has been proposed by Taylor (1961). He has shown that the variability in population abundance of a species (V) can be related to the average population density (m) by a simple power law: $V=am^b$ (where a and b are constants). Like the method of Iwao, it was also designed to analyse the relationship between variance and mean density of conspecific populations occurring at different densities. Applying the relationship to the variance and mean abundance of species in the seed bank community we obtain the relationship (Fig.3): $V = 2.846\ m^{1.228}$, or $lnV = 1.046 + 1.228\ lnm$ ($r^2 = 0.96, p < 0.001$). Interpreting the meaning of Taylor graphs is fraught with problems (Soberón & Loevinsohn, 1987) but it can be concluded from the position of the line in Fig.3, relative to the line of variance = mean, that the pattern of aggregation changes with the mean; the species with low densities tend to have a random dispersion of seeds while the abundant species have a more aggregated pattern. The slope of the line (1.229) which gives a measure of how the pattern of proportional variation changes with the mean indicates that the proportional variation decreases with the mean. The reason for this is unclear but it could be that density-dependent mechanisms lead to a more even distribution of seeds. Dessaint *et al* (1991) similarly found that species with higher densities had more aggregated patterns and that the variability in patchiness was greater in species with low densities. The generality of such patterns needs to be further explored.

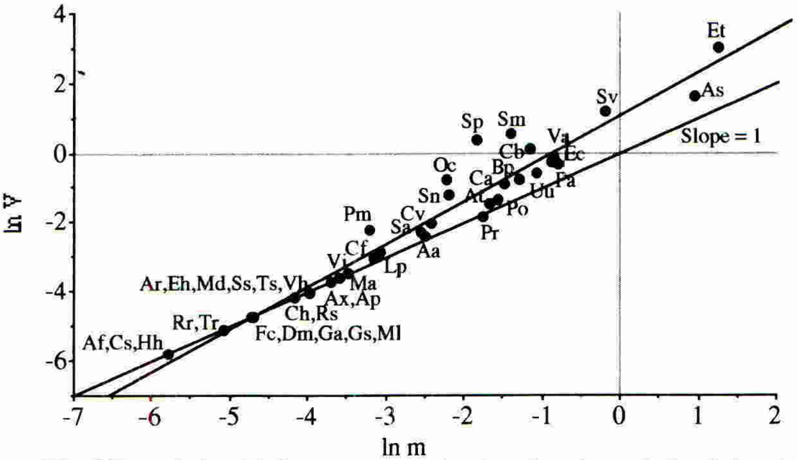

Fig. 3 The relationship between mean density of seed population (*m*) and sample variance (*V*). See Fig.1 for species codes.

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DOES ROTATIONAL FALLOW CAUSE WEED PROBLEMS IN SUBSEQUENT CROPS?

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ABSTRACT

In a set-aside programme, a field trial was carried out to investigate the effect of natural regeneration and various autumn- and spring-sown cover crops on the weed seed bank. The number of weed seeds in the soil was determined before and after the fallow period. The growth rate for different weed species in the rotational fallow was calculated. To estimate the impact of the seed rain on weed infestation in the subsequent crop, the growth rates were compared with the rates in crops with and without chemical weed control. For the weeds in total, the growth rates of the seed bank in set-aside and in crops were similar, if weed seeding was reduced by competitive cover crops. For individual weed species a significant reduction of seeding during set-aside was not achieved and the seed bank increased. In general, a well managed rotational fallow did not cause severe weed problems in subsequent crops. Beside the set-aside management, however, efficient weed control is necessary to avoid further problems with weed infestation in the following crops.

INTRODUCTION

Since 1988 farmers have been able to take part in the set-aside programme of the EC. The aim of the programme is to reduce surpluses of arable crops. Fallowed land must be covered either with sown plants or with natural regeneration and no fertilizers and pesticides may be used. During the fallow, the vegetation must be managed to avoid severe weed problems in the subsequent crops. Therefore, seeding of weeds and cover crops must be prevented by cutting, but a complete prevention can hardly be achieved (Lechner *et al.* 1992).

To estimate the impact of the weed seed rain during the fallow on weed infestation in the subsequent crop, and to give an answer to the posed question, the growth rates of various weed species in a rotational fallow were calculated and compared with the rates of conventionally managed crops. The growth rate describes the alteration of the weed seed bank in the soil from one year to the next.

MATERIALS AND METHODS

The set-aside field trial (1990/91) included winter cover crops: winter rape (*Brassica napus*), winter rye (*Secale cereale*), subterranean clover (*Trifolium subterraneum*), white clover/perennial ryegrass *(Trifolium repens/Lolium perenne*) and spring cover crops: white mustard (*Sinapis alba*), oats (*Avena fatua*), field bean (*Vicia faba*). In Germany, harvestable crops were allowed as cover crops until 1992. In addition to the cover crops, plots with natural regeneration were included. The trial was carried out as a complete randomised block design with 3 replications. The autumn-sown cover crops and the plots with natural regeneration which started growing from autumn were cut in June, the spring covers in July. The plant material was left on the field. The weed seed bank was determined before and after fallow. Thirty soil samples per plot (diameter 4 cm, depth of 25 cm) were bulked and placed in shallow dishes in a greenhouse. Emerged seedlings were recorded several times over a period of 1 year (Lechner *et al.* 1993) and the growth rate was calculated as quotient of the number of seeds in the year t_{+1} and t.

These growth rates were compared with corresponding data of two long-term field trials which were carried out to investigate the effect of different cropping systems on the population dynamics of weeds. The crops used in the first experiment were winter wheat and field bean, with and without chemical weed control (Zwerger *et al.* 1990) and in the second one winter wheat, winter rape and spring barley without weed control (Amann *et al.* 1992). In these trials the weed seed bank was estimated at the beginning of successive cropping periods as described above and the growth rates were calculated.

The growth rates for the weeds in the crops will be presented as box-and-whisker-plots. The bottom and top edges of the box are located at the sample 25th and 75th percentiles; ◆ symbolizes the sample median, ● the sample mean. The central vertical lines extend from the box as far as the data extend, to a distance of at most 1.5 interquartile ranges. Any value more extreme than this is marked with a ○, if it is within 3 interquartile ranges of the box, or with a *, if it exceeds this value (SAS, Release 6.04). Such presentation permits illustration of not only the sample mean, but also of the variation and the distribution of the single values within the sample. For the set-aside, the data base was not large enough to calculate box-and-whisker-plots, and therefore the results are presented as mean values.

All three experiments were carried out on fields near Stuttgart-Hohenheim with a similar weed species composition, but not in the same years.

RESULTS AND DISCUSSION

In all experiments species composition was typical for crop rotations with a high proportion of winter wheat. The main weed species were *Alopecurus myosuroides*, *Lamium purpureum*, *Stellaria media* and *Veronica persica*. These species occurred in all trials and the number was sufficient to compare the growth rates with one another, while other species such as *Capsella bursa-pastoris*, *Chamomilla recutita*, *Fallopia convolvulus*, *Galium aparine* or *Poa annua* did not occur constantly. Before set-aside the weed seed bank varied from 2200 to 5700 seeds/m² and after the fallow from 5600 to 32400 seeds/m². Weeds such as *Elymus repens* or *Cirsium arvense* which are difficult to control were not present in these field trials.

The growth rate in set-aside depended strongly on the treatments. In general, autumn treatments reached higher values than spring treatments. Responsible for this difference was a shallow soil cultivation before sowing the spring cover crops, which destroyed the emerging weeds. Within the autumn and spring treatments, the natural regeneration led to growth rates up to 12 and 4, respectively, while with cover crops, except winter rye, the rates were much lower. In general, the set-aside treatments caused similar growth rates as observed in crops without weed control. With appropriate set-aside treatments, however, like the clover/grass mixture, it is possible to keep the growth rate as low as in crops with weed control (Fig. 1).

With regard to single weed species, the results obtained for *L. purpureum* and *V. persica* were similar to those for the weeds in total. For both species, the autumn treatments, especially the natural regeneration, resulted in the highest growth rates, and were significantly higher than the average rates in the crops. However, the clover/grass mixture did not limit *L.*

purpureum as much as *V. persica*. This was probably due to a good development of *L. purpureum* during autumn and its seed production before cutting (Fig. 2).

In contrast to the weed species mentioned above and the weeds in total, *A. myosuroides* and *S. media* had different growth rates in set-aside and crops, although the ranking in the set-aside treatments was similar. The growth rates of *A. myosuroides* were smaller in the set-aside than in the crops, especially in cereals. Because of its erect habit *A. myosuroides* was destroyed by cutting in the set-aside while in the crops it could develop uninterrupted. *S. media* showed significantly higher growth rates in the set-aside than in the crops, especially in the less competitive winter cover crops and in the natural regenerations. *S. media* plants were hardly influenced by cutting because of their creeping growth habit and after cutting they could develop very well without competition of the cover crops. In addition, a second generation led to extreme growth rates (Fig. 3).

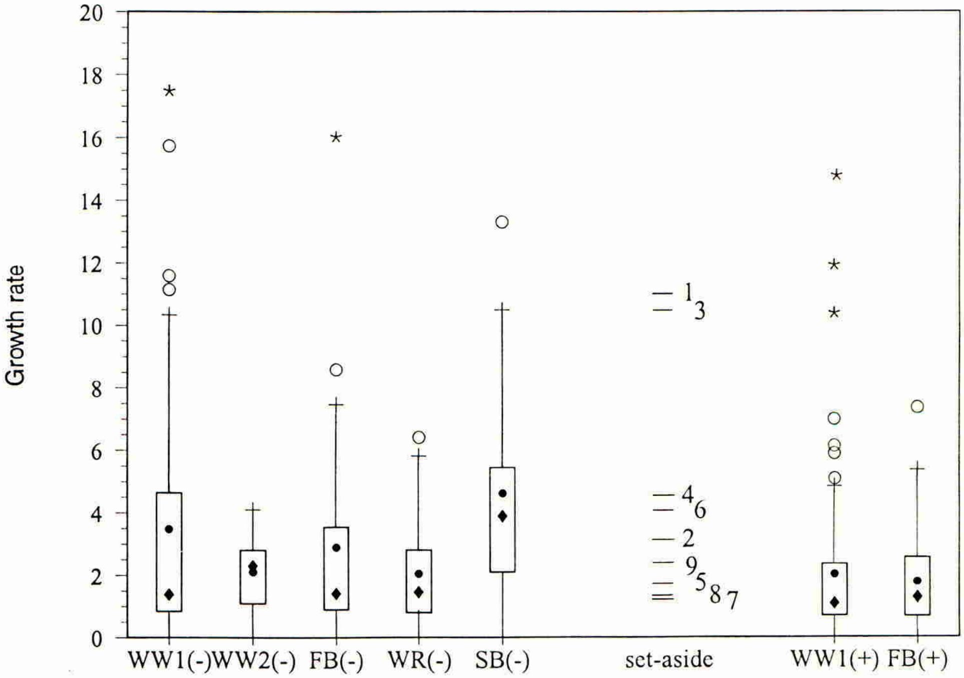

Figure 1. Growth rate of weeds in set-aside and different crops (calculated at the base of the seed bank in the soil).
The population remains constant if the growth rate = 1. If the growth rate is > 1 the population increases, if it is < 1 (but ≥ 0) the population decreases.

crops: WW1/2 = winter wheat (experiment 1/2); FB = field bean; WR = winter rape; SB = spring barley; Weed control: (-) = without; (+) = with

set-aside:
1 = natural regeneration (autumn)
2 = winter rape
3 = winter rye
4 = subterranean clover
5 = white clover/perennial ryegrass
6 = natural regeneration (spring)
7 = white mustard
8 = oats
9 = field bean

symbols: see text

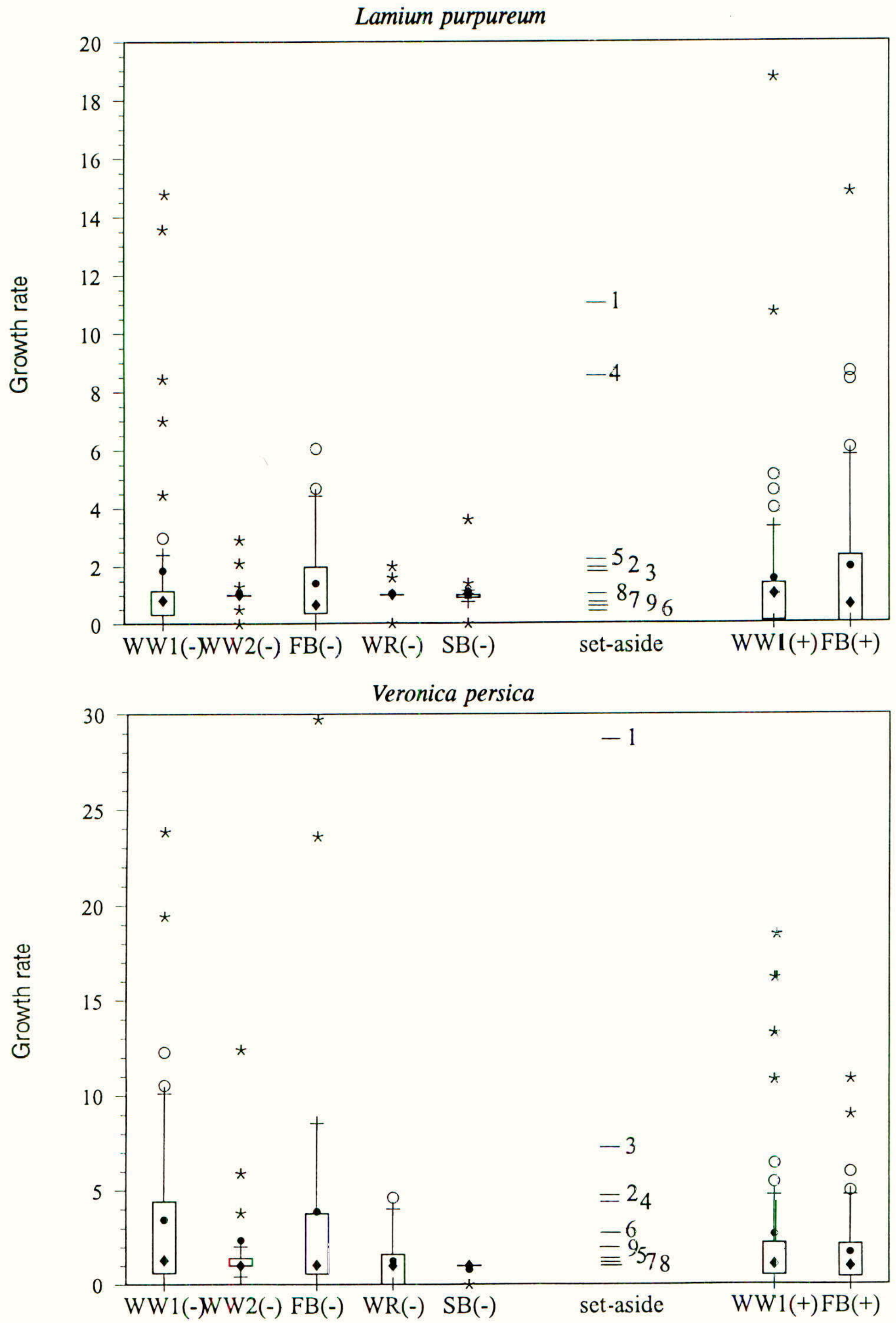

Figure 2. Growth rate of *Lamium purpureum* and *Veronica persica* in the set-aside and in different crops (For explanation see Figure 1).

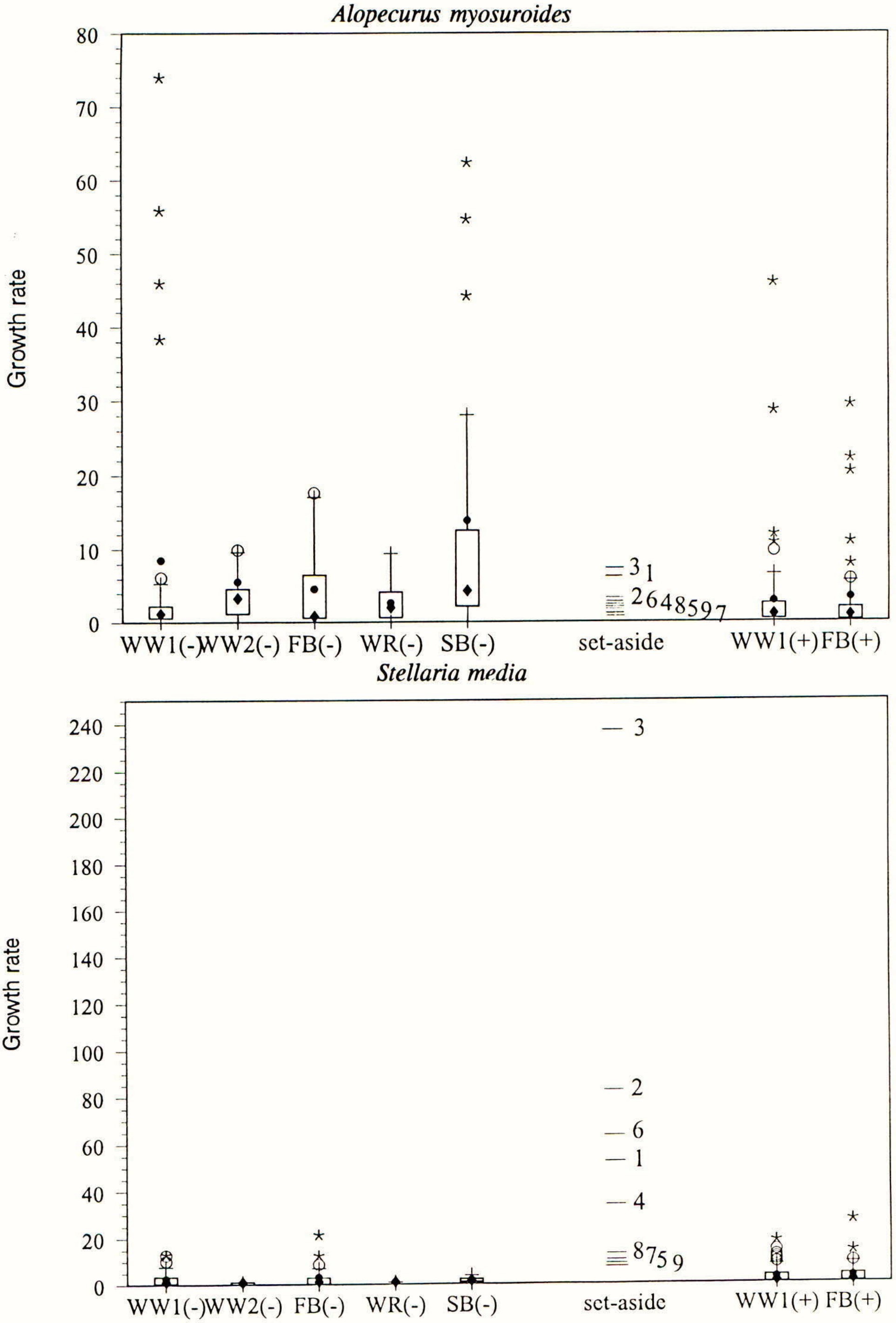

Figure 3. Growth rate of *Alopecurus myosuroides* and *Stellaria media* in the set-aside and in different crops (For explanation see Figure 1).

CONCLUSIONS

Farmers, participating in the set-aside programme, do not want an increase in weed infestation by fallowing. Various experiments have shown that cutting and the use of competitive cover crops (especially if they regenerate after cutting) are suitable for weed management in set-aside (Clarke and Froud-Williams 1989, Fisher and Davies 1991, Forche 1991). However, no setaside treatment can prevent weed seeding completely and therefore the weed seed bank in the soil increases after fallow (Lechner *et al.* 1993). As shown with the growth rates, the increase of the seed bank after fallow was, in general, higher in natural regeneration than in cover crops. The growth rates of autumn natural regeneration and of less competitive cover crops were higher than the growth rates of conventionally managed crops, if the mean values were considered, but similiar with the extreme values.

The comparison made between growth rates in set-aside and in crops demonstrates that there are appropriate set-aside treatments which keep the growth rate for most of the weed species as low as in crops with weed control. From this, it is concluded that severe weed problems are not to be expected after well managed rotational fallow. Even if badly managed set-aside leads to high growth rates, they are still similar to situations in crops, where weed control measures have failed. From experience it is known, that such events do not create bigger problems in subsequent crops, if effective control measures are available. However, once the weed seed bank has been build up, it will take a long time of intensive weed control to reduce it.

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SEEDBANK PERSISTENCE OF FIVE ARABLE WEED SPECIES IN AUTUMN-SOWN CROPS

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ABSTRACT

The decline in natural seedbanks of five arable weed species was studied in a succession of autumn-sown crops in fields ploughed annually for 3-4 years, during which period no return of weed seeds to the soil was permitted. Numbers of viable seeds of *S. media* declined more slowly than those of *P. annua*, *C. bursa-pastoris*, *C. album* and *P. aviculare*. Exponential curves indicated a time to 99% decline of 11.1 years for *S. media* and between 4.3 and 6.5 years for the other species. Seedling production represented only a very minor proportion of the available seedbank in any one year. Weed seedlings emerged in greatest numbers in the later years of the experiments, possibly due to earlier seedbed preparation and more favourable growing conditions in autumn in these years. The results are compared with data for a range of other arable weeds and discussed in relation to weed control strategies.

INTRODUCTION

An understanding of the persistence of weed seedbanks is essential to the formulation of rotational strategies for the management of weeds in cereals. This is particularly important at a time when there is increasing economic and environmental pressure on farmers to reduce their herbicide inputs, whether by reducing dose or by the use of thresholds to determine the need for spray treatment in an individual crop (Lawson, 1993). Seeds produced by uncontrolled weeds will add to the existing seedbank, thereby increasing the potential problems of weeds in crops later in the rotation. Wilson & Lawson (1992) examined the persistence in the soil of seven arable broad-leaved species - *Galium aparine*, *Papaver rhoeas*, *Lamium purpureum*, *Myosotis arvensis*, *Veronica persica*, *Viola arvensis* and *Veronica hederifolia* - in a succession of autumn-sown crops following a single year's seeding in two experiments where competition between wheat crops and sown stands of individual weed species had been studied. The weeds were allowed to seed in these experiments and the fate of these seeds was monitored over a period of years. At the same time records were made of the decline of components of the seedbank of indigenous species in both experiments. *Stellaria media* had also been sown in individual plots in the original experiments, before it was realised that indigenous seeds of this species were already present in large and very variable numbers across both sites. It was, therefore, not possible to identify the origin of seeds or plants on sown plots and this species was excluded from the earlier paper. Our second paper examines the persistence of *S. media*, regardless of origin, and of *Poa annua*, *Capsella-bursa-pastoris*, *Chenopodium album* and *Polygonum aviculare* in the natural seedbank through three or four autumn-sown crops in which no further seed return to the soil was permitted.

MATERIALS AND METHODS

The experiments were carried out at two sites on sandy loam soils at Long Ashton Research Station. Soil seedbanks were first sampled in 1987 (Experiment 1) or 1988 (Experiment 2) following the sowing of an autumn crop. Both sites were ploughed annually to a depth of 20 cm in late summer or early autumn. They were cropped continuously with winter wheat, except for a crop of winter oilseed rape grown in the last year (1990) of Experiment 1. Further samples of soil seedbanks were taken every autumn and counts were made of weed seedlings (prior to spraying herbicides) for a total of four years (Experiment 1) and three years (Experiment 2). The use of broad-spectrum prophylactic herbicide treatments, supplemented by hand-weeding, ensured that no weeds survived to replenish the seedbanks.

Plots were laid out in split-plot, randomised block design with four replicates. Sown individual species had been the main treatment factor, with different weed densities as a secondary factor, giving a total of 64 and 128 plots for recording of *S. media* and the other naturally-occurring species in Experiments 1 and 2 respectively. Sub-plot size was 3 m by 3 m. Seedbanks were determined by taking ten soil cores, 2.54 cm diameter and 20 cm deep from each plot. The cores were bulked and stored at -20°C; after thawing, the samples were mixed thoroughly before three 200 ml sub-samples were extracted and analysed for weed seed content by sieving and flotation (Roberts & Ricketts, 1979). Viable weed seeds were identified and counted (Lawson *et al.*, 1988). Weed seedling numbers were recorded on the central square metre of each sub-plot. Dates of crop planting, weed assessment and soil sampling and details of herbicides used were presented in our earlier paper (Wilson & Lawson, 1992) and are not repeated here.

Both weed and seed data were subjected to analysis of variance after square root transformation. For each experiment, and each species within an experiment, an exponential curve, decaying towards zero, was fitted to the mean seed number. Annual rates of decline and the time in years to 50% and 99% decline were derived. Weighted means were obtained (weights were inverse S.E.s) together with their standard errors.

RESULTS

Numbers of seeds of the five species recovered from the soil and of seedlings produced each year are shown in Tables 1 and 2 respectively. Data for *S. media* are presented with and without the inclusion of records from sown plots. In Experiment 1, only 4 out of a total of 64 plots had been sown with this species in 1987, while in Experiment 2 in 1988 the figure was 12 out of 128. Exclusion of the sown plots in the analysis made little difference to the treatment means and slightly increased the S.E.D. in three out of four cases. It was decided, therefore, to take advantage of the increased degrees of freedom and to maintain uniformity with the records for other species by using values from all plots to fit the exponential curve for this species.

The effect of years was significant at the 0.1% level for both seeds and weeds of all species in each experiment. In Experiment 1 seed numbers showed the greatest decline during the first 12 months, whereas in Experiment 2 the

TABLE 1. Persistence of seedbanks in successive crops

No. seeds/m^2 (to 20 cm depth) - $\sqrt{(x + 0.375)}$

Species	Expt no.	1987	1988	1989	1990	S.E.D.	D.F.
S. media (a)*	1	105.9	61.0	52.0	55.6	3.50	168
	2	-	38.1	34.8	27.3	2.02	264
S. media (b)**	1	92.1	57.2	49.1	51.6	3.22	147
	2	-	33.6	31.2	23.7	2.18	231
P. annua	1	25.9	10.9	8.8	7.4	1.98	168
	2	-	21.5	22.1	15.2	1.68	264
C. bursa-pastoris	1	13.6	9.8	6.1	5.4	1.86	168
	2	-	6.6	4.8	3.1	1.04	264
C. album	1	31.3	13.4	15.3	12.5	2.43	168
P. aviculare	1	11.6	4.9	5.1	3.6	1.45	168

TABLE 2. Weed seedling emergence in successive crops

No. seedlings/m^2 - $\sqrt{(x + 0.375)}$

Species	Expt no.	1987	1988	1989	1990	S.E.D.	D.F.
S. media (a)*	1	2.89	2.28	8.15	6.34	0.265	168
	2	-	1.15	6.11	3.78	0.119	264
S. media (b)**	1	2.68	2.26	8.28	6.35	0.284	147
	2	-	1.14	6.10	3.77	0.128	231
C. bursa-pastoris	1	0.62	0.64	1.89	2.14	0.142	168
	2	-	0.64	1.00	0.99	0.055	264
C. album	1	0.61	0.61	0.62	0.78	0.033	168

* Including sown plots
** Excluding sown plots

decline was more gradual. Table 3 shows rates of decline of seeds of individual species, using fitted curves based on both experiments for *S. media*, *P. annua* and *C. bursa-pastoris* and Experiment 1 only for *C. album* and *P. aviculare*. The results indicate that seeds of *S. media* were by far the most persistent, showing an annual rate of loss of only 30% and requiring 1.7 and 11.1 years to decline by 50 and 99% respectively. Numbers of seeds of the other species declined by between 50 and 60% per year; they took between 0.7 and 1.0 years to decline by 50% and would have taken between 4.3 and 6.5 years

TABLE 3. Rate of decline of seedbanks, based on fitted exponential curves

Species	% Decline/year				No. of years to decline			
	Expt no.		Weighted		50%		99%	
	1	2	Mean	S.E.±	Mean	S.E.±	Mean	S.E.±
*S. media**	41.9	27.1	30.0	5.30	1.7	0.37	11.1	2.44
P. annua	66.6	26.1	54.8	6.52	0.7	0.13	4.3	0.88
C. bursa-pastoris	50.1	51.5	50.6	9.09	1.0	0.26	6.5	1.70
*C. album***	51.7	-	51.7	7.92	0.9	0.22	6.3	1.43
*P. aviculare***	60.1	-	60.1	13.20	0.8	0.27	5.0	1.81

* Including sown plots
** Based on only one site (Experiment 1)

to virtually disappear from the seedbank.

Numbers of seedlings of *S. media* were much greater than those of other species and they were more abundant in 1989 and 1990 than in earlier years. Nevertheless, only 1.1% of the original seedbank of *S. media* produced seedlings over four years in Experiment 1 and only 3.6% over three years in Experiment 2. The relevant figures for the much smaller seedbank of *C. bursa-pastoris* were 1.3 and 0.2% respectively. Seedlings of *P. annua* were not recorded, since the original project concerned only broad-leaved weed species. No *P. aviculare* seedlings and very few *C. album* seedlings were found in the winter crops grown in Experiment 1.

DISCUSSION

The behaviour of the indigenous seedbanks of the five species studied in winter cropping rotations can usefully be compared with that of the seedbanks of sown species in the same experiments. To facilitate this, Table 4 shows the seedbank decline of the latter species (Wilson & Lawson, 1992), presented in the same format as in Table 3. The vast majority of seeds of the sown species had been freshly produced, shed and ploughed in shortly before the first soil sampling date, whereas the naturally occurring species had not been allowed to seed in that year and their seeds may have been in the soil for a period of years. Nevertheless, the pattern of decline of four of the indigenous species fell within the middle range (4.3-6.5 years to 99% decline) shown by the sown species. *S. media* was comparable with the most persistent of the sown species examined - *V. arvensis*, requiring more than 10 years to achieve 99% decline. The similarity of the two sets of data suggests that the age of seed may have had relatively little to do with their rate of decline in the soil. The large drop in seed numbers of sown species in the first year of Experiment 1 was matched by that of the indigenous species and may also have been related to seasonal factors.

Seedling emergence by indigenous species also followed a pattern similar to that of the sown species, with increasing seedling numbers produced as the seedbanks declined (Wilson & Lawson, 1992). For the sown species, the lack of seedling production in the first autumn was attributed to ploughing having placed most seeds too deep in the soil for successful emergence. The data for the indigenous species suggests that this may have been only one of the factors

TABLE 4. Rate of decline of seedbanks of sown species based on fitted exponential curves (from Wilson & Lawson, 1992)

Species	% Decline/year				No. of years to decline			
	Expt no.		Weighted		50%		99%	
	1	2	Mean	S.E.±	Mean	S.E.±	Mean	S.E.±
G. aparine	55.5	85.4	65.9	4.07	0.5	0.07	3.6	0.47
P. rhoeas	24.9	43.9	34.7	6.53	1.3	0.32	8.7	2.13
L. purpureum	39.1	59.5	54.3	4.37	0.8	0.10	5.4	0.68
M. arvensis	60.0	34.8	43.5	5.35	0.9	0.17	6.1	1.12
V. persica	58.3	36.0	45.8	6.92	0.9	0.21	6.1	1.37
V. arvensis	36.4	36.4	36.4	3.74	1.5	0.20	10.2	1.32
V. hederifolia	56.1	59.9	57.4	7.12	0.8	0.16	5.4	1.06

involved, since the latter seeds would already have been fairly evenly distributed in the top 20 cm of soil; they still produced few if any seedlings in the first autumn. This reinforces the suggestion made in our earlier paper that weed emergence may also have been affected by date of seedbed preparation. The dates of crop sowing in Experiment 1 were 6 Nov. 1987, 17 Oct. 1988, 3 Oct. 1989 and 29 Aug. 1990, while for Experiment 2 they were 17 Oct. 1988, 24 Sep. 1989 and 27 Sep. 1990. Better emergence of seedlings of most species in 1989 and 1990 may have had more to do with early seedbed preparation and/or more favourable growing conditions than with the rate of decline or age of the seedbank.

The data for all species show the difficulty of predicting likely weed populations from the size of the seedbank at any one time. The existence of even a small seedbank offers the potential for trouble in future crops if conditions favour germination. In a series of experiments on reducing herbicide inputs in cereals (Lawson, 1993), the failure adequately to control small numbers of seedlings of *S. media* in winter cereals resulted in major seedbank expansion and severe consequences for the rotational weed control strategy.

Most of the sown or indigenous species of weeds referred to in this study regularly germinate in autumn seedbeds (Mortimer, 1989). However, *C. album* and *P. aviculare* are more likely to germinate in spring and would not have been expected to appear in winter crops where the soil was undisturbed in spring. The finding that only a small percentage of the indigenous and sown species capable of germinating in autumn did so is in agreement with the findings of Roberts (1981) on the quantitative relationships between seedling numbers and seedbanks.

Data on the persistence of both the sown and the indigenous species in the two experiments described herein provide useful information for devising long-term strategies for weed control in winter cropping rotations. The three-fold difference between the relatively short persistence of species such as *G. aparine* and *P. annua* and the very much longer survival of *V. arvensis* and *S. media* must be taken into account when assessing the consequences of allowing weeds to seed. Further experiments are in progress comparing the effects of tine cultivation with ploughing and of spring as opposed to winter cropping on seedbank persistence and seedling emergence.

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DECLINE OF YELLOW NUTSEDGE (*CYPERUS ESCULENTUS*) WHEN TUBER FORMATION IS PREVENTED

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ABSTRACT

Population decline of Yellow Nutsedge (*Cyperus esculentus*) was studied under field conditions in a longterm experiment. Formation of new tubers was prevented by repeated control of primary shoots with glyphosate and mechanical control.
The effects were determined by counting regrowth before each re-treatment. The experiment was carried out on a field with a dense natural infestation. Even after one year of intensive control, the number of Nutsedge plants had been drastically reduced. Complete eradication was not reached; a few tubers remained dormant in the soil during at least six years.

INTRODUCTION

Yellow Nutsedge (*Cyperus esculentus*) is a widespread weed throughout the world from the sub-tropics to temperate climates, and has great agricultural importance (Bendixen & Nandihalli, 1987). The species received little attention in Europe although it occurred in the Mediterranean area, where herbicide dependent, large scale agriculture was not yet important. However,in the early eighties alarming reports about considerable problems in the South West of France were presented by Morin (1984). At the same time the weed had appeared in the Netherlands, where it was found to be locally well established after introduction via gladiolus cormlets from the USA (Naber & Rotteveel, 1986a). In the Netherlands the weed was soon recognised as a very aggressive invader, worth an eradication campaign, taking into consideration the initially small infested acreage (Naber & Rotteveel, 1986b).

In eradication programmes for annual weeds, prevention of seed formation is the most important factor. This leads to an exponential decline of the number of plants. Stimulating germination of the seeds in the soil by repeated soil cultivations within one season gives an even quicker decline (Roberts, 1983). In an eradication campaign on the perennial Yellow

Nutsedge, the prevention of tuber formation is of primary importance. Propagation through seed does not seem to occur in the Netherlands and the plant itself and its rhizomes do not survive winter. The population dynamics of the weed has been studied by several workers (Cloutier *et al.*, 1988; Van Groenendael & Habekotté, 1988). Their models show that even very few surviving tubers may rebuild a population very quickly under favourable circumstances, due to the high propagation capacity of the species.

Prevention of tuber formation is possible by regularly killing all primary sprouts (Keeley *et al.*, 1986). Glyphosate was shown to be an effective leaf applied herbicide on Nutsedge. However after chemical control re-sprouting from tubers occurs and therefore more foliage treatments are needed within one season. The time emerged plants need to produce new tubers, depends on such factors as temperature and day length, but a period shorter than 3 weeks has not been observed in the Netherlands.

In this paper we present results of a study to develop strategies aimed at eradication of Yellow Nutsedge. This long-term study was focussed on the decline of a field population of Yellow Nutsedge, enforced by repeated chemical and mechanical control measures under non-crop conditions. We reported a related eradication study, but under cropped conditions, earlier (Rotteveel & Naber, 1993).

MATERIALS AND METHODS

The long-term experiment in a non-crop situation was started in 1985 and lasted until 1990. In 1991 final observations were carried out in the farmer's crop (maize). The aim was to study the accumulation of effects caused by yearly treatments of chemical and/or mechanical control of primary shoots of *C. esculentus*. We intended to continue to zero infestation in at least one treatment. The experiment consis-ted of four randomised treatments in four blocks, the plot size was 10x10 m^2. Between the plots 1 m wide buffers were kept meticulously weedfree. Mechanical equipment was cleaned carefully before being moved from one treatment to another.

Treatments:

A. Mechanical control with a rotavator, when the first plants start to produce rhizomes and repeated as often as needed.
B. Glyphosate (2.88 kg/ha a.i.), when the first plants start to produce rhizomes and repeated as often as needed.
C. First treatment as in A (Mechanical), followed by treatment as in B (Chemical), followed by A etc.
D. First treatment as in B (Chemical), followed by A (Mechanical), followed by B etc., but modified 1987-1990.

The experiment was located in Gemert, Noord Brabant on a mixed chicken/arable farm as is common in the area. Nutsedge infestation was first found on this field by the authors in 1981 in a gladiolus crop and very likely originated from the gladiolus planting material. The soil is a shallow, very light sandy soil; undisturbed sand is present at 25-30 cm depth. In wintertime as well as in wet spells in summer, the soil can be very wet, due to the high groundwater level at about 1.20 m and the rather fine sand. In dry spells the soil becomes very dry on the surface. The field has been used for arable farming, mainly silage maize, for about 30 years; it is a reclaimed heath soil. Nutrient status now is comparatively high because of the abundant use of liquid manure (slurry).

Treatments A, B and C were carried out unchanged over the whole period of the experiment. Treatment D was modified from 1987 to 1990; little additional information was gained and therefore the results of the latter period will be omitted. During the whole experimental period treatment B received almost 75 kg/ha a.i. glyphosate. In 1987 we feared that the undisturbed sub-soil might shelter dormant tubers for a longer time. We cultivated two blocks with a chisel plough to a depth of 30 cm. No effects of this deep soil cultivation were seen in that year or later and this partial treatment will be further omitted.

The accurate detection of tuber populations present in the soil is practically impossible, especially at low densities, because high numbers of soil samples have to be taken and each sample has to be quite large in order to produce reliable data. Therefore initial infestations were determined by counting primary shoots only. The possibility remains open, that the number of shoots does not represent the number of tubers in the soil very well, because the amount of dormant tubers is not known.

Before the first treatment June 18, 1985, the number of Nutsedge shoots present was determined by counting 10 quadrats of 0.25 m^2 per plot. Because the Nutsedge density was high and the plants grew vigorously, it was difficult to count shoot numbers exactly during that season. In all following years we counted shoot numbers before every treatment and two weeks after the last treatment of the season. These counts were always taken from the full plots.

From 1985-1990 no crops were grown and no fertiliser was applied. In order to counter soil structure deterioration, which was very serious on treatment A (Mechanical), winter rye was sown by hand every autumn after finishing Nutsedge observations and was killed again with paraquat before first Nutsedge emergence in May.

RESULTS

At the beginning of the experiment in 1985 the number of primary shoots in June varied roughly from 200 - 300 per m^2.

The initial density per plot was not significantly different between treatments (P = 0.899). During the seven years the experiment lasted shoots have been counted on 42 occasions. Because the shoots were counted 5-7 times a year, the results of these observations are presented here as year-totals per treatment in Figure 1a and 1b.

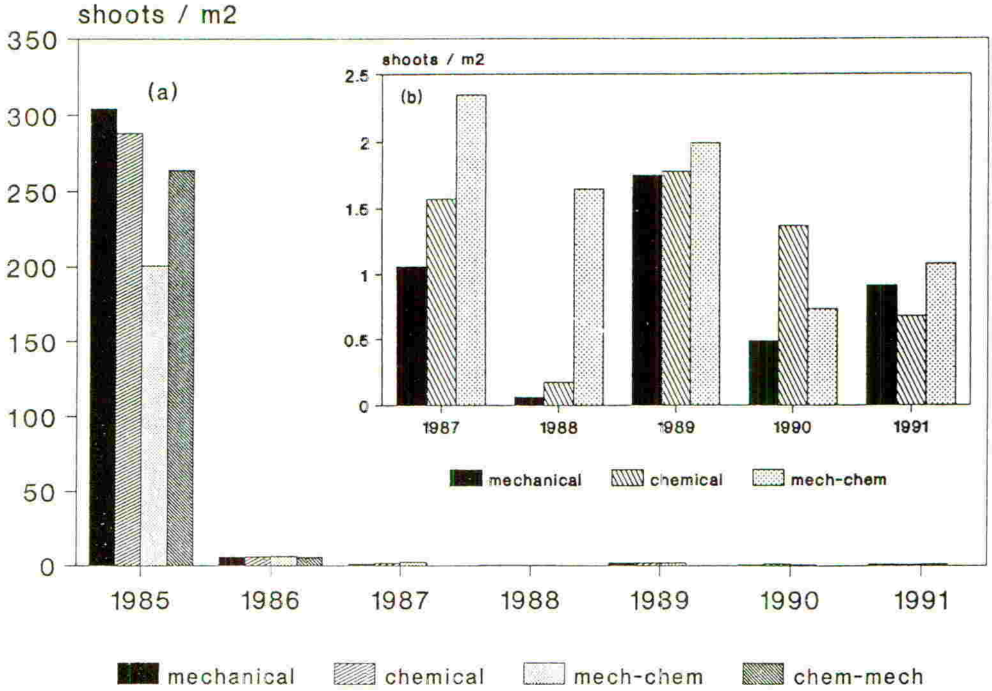

FIGURE 1a, 1b **Number of primary shoots of Cyperus esculentus from 1985-1991 after intensive control preventing new tuber formation. Fig 1b (window) repeats the results from 1987-1991 on an different scale at the Y-axis.**

After one year (1985) of intensive control the amount of Yellow Nutsedge sprouts was reduced by 97-99 % (Figure 1a). In the next year (1986) a further reduction of 50-75 % was obtained. From 1987 onwards the population did not, or only gradually decrease to a level of 1-2 plants per m^2 (Figure 1b). In each year the total number of plants in Treatments A, B, C and D (1986 only) were statistically compared (ANOVA, SPSS/PC-+), but no significant differences in weed control were seen.

An interesting observation was that as time passed the remaining Nutsedge tended to sprout later than on untreated fields. In the last years of the experiment virtually all sprouts examined originated from a depth greater than 20 cm and often at the line between topsoil and sand subsoil. These tubers were often surprisingly large. According to Ter Borg &

Schippers (1992) the population of *C.esculentus* in this field is the var.*macrostachyus*, penetrating into deeper layers, but being less frost resistant and less tolerant to shade than var.*leptostachyus*.

Nutsedge developed poorly during the experimental period, neither flowering nor tuberisation was found on any observation date. Although seed production has been observed in the past on the farmer's field, no seedlings have ever been found in this experiment.

DISCUSSION

The aim of the experiment was to develop strategies to eradicate *Cyperus esculentus* on infested fields. Prevention of new tuber formation, the main factor in such an eradication approach, was obtained by means of chemical and mechanical control of primary shoots. Even after one year of intensive control in the non-crop situation, the number of Yellow Nutsedge plants had been drastically reduced. After two years of control the population density declined rapidly. During the next years the number of plants hardly decreased further, indicating that it is easier to reduce a heavy infestation (200-300 plants per m^2) to a light one (1-2 plants per m^2), than a light infestation to zero.

The first years had similar, relatively cold and late springs, which did not favour Nutsedge growth. In 1988 hardly any shoots were found and eradication seemed within reach. From 1989 onward spring and summer, and the whole year-average temperatures were above normal and Nutsedge appeared in much higher numbers in 1989, after which a decline followed in later years.

Treatment A (mechanical control) had slightly, but not significantly, better results than Treatment B (glyphosate), and Treatment C (mechanical/ chemical). Treatment C was expected to be the best, combining a stimulation of sprouting of tubers in the soil by the rotavating operation, with mechanical and chemical control of the emerging shoots.

In Treatment A soil structure was thoroughly destroyed after 7 years of regular rotavating without any crop, or weed growth. In Treatment B (glyphosate) soil structure remained intact, also because of the protecting thin moss cover which developed on these plots.

In 1991 the farmer ploughed the field to a greater depth than the rotavation had done (about 20-25 cm) and cultivated a maize crop. In this year we did our last observation and found slightly, but not significantly, more Nutsedge in Treatments A (mechanical) and C (mechanical/chemical), than in Treatment B (chemical).

We are not able to conclude how long dormant tubers can survive in the soil. In the later years we observed on many occasions that shoots originated from large tubers in the subsoil. We have shown that under these particular field circumstances a tiny proportion of the initial amount of tubers formed in 1984 or earlier, was still alive and sprouting in 1991. This means survival in the soil for at least seven years. Exhaustion of the tuberbank in the soil took more time than was expected, but may depend on the variety of *C. esculentus*.

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EFFECT OF CULTIVATIONS AND SOIL TYPE ON THE SEED EMERGENCE OF BARREN BROME, MEADOW BROME AND WINTER BARLEY

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ABSTRACT

An experiment with sites in Cambridgeshire and Hampshire was established in the autumn of 1988 to investigate the effect of cultivation on emergence of different stocks of barren brome (*Bromus sterilis*) and winter barley, and one stock of meadow brome (*Bromus commutatus*). Over a period of three years when there was no seed return, ploughing to a depth of 20 cm, gave absolute control of these weeds in years two and three at Boxworth and virtually complete control at Bridgets. In the first year ploughing reduced emergence by 99 per cent compared with about 30 per cent with tine cultivation to a depth of 5-20 cm. Levels of emergence of two stocks of barren brome and one of meadow brome varied slightly over a three year period and between sites. Short and long dormancy stocks of winter barley showed patterns of emergence similar to brome. Considerably more emerged in the autumn in which they were incorporated.

INTRODUCTION

Brome grasses increased dramatically in the late 1980s, having been favoured by dry autumns in 1984 and 1985 (and to a lesser extent, in 1986) when germination was delayed well into the autumn resulting in heavy infestations emerging with the crop. In the 1989 BCPC-funded survey of brome grasses 44 per cent of crops in England and Wales were found to have brome grasses as weeds in the field centres and headlands (Cussans *et al*, 1989). The distribution of the bromes was very strongly biased towards the field margins and headlands although 12 per cent of field centres were infested.

Early work indicated that seeds of *Bromus* species had little dormancy, short persistence in the soil (Froud-Williams, 1983) and were unable to emerge when ploughed in to a depth of more than 12cm (Froud-Williams, 1981). Therefore, these species should persist only in a very specific husbandry system; where continuous, early sown winter cereals were established without mouldboard ploughing. However, there were an increasing number

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of reports of field behaviour which did not fit into this predicted pattern; protracted germination, survival from mouldboard ploughing and survival beyond one year without seed production. These specific reports were linked with a general belief that these species were increasing in severity despite an increase in the use of mouldboard ploughing. Subsequent research has found that some stocks have more dormancy than others (Peters, 1990).

MATERIALS AND METHODS

The experiment was started in September 1988, with sites at ADAS Boxworth, Cambridgeshire, and ADAS Bridgets, Hampshire, on areas free from brome grasses or volunteer barley. The soil texture at Boxworth is a calcareous silty clay loam and at Bridgets a calcareous medium silty loam.

The experimental design was three randomised replicates with cultivation treatments on whole plots and weed species on sub-plots. Whole plots measured 20 m x 17 m and sub-plots 4 m x 2 m. Seed of brome grasses was collected from standing crops in July/August 1988. The "weed" seeds were broadcast onto the soil surface immediately prior to the primary cultivation in the first year at a rate of 10,000 seeds/square metre for the brome and 250 seeds/square metre for the barley.

The weed species were indigenous barren brome (*Bromus sterilis*); non-indigenous barren brome from Long Ashton Research Station, Bristol, (Boxworth only); meadow brome (*Bromus commutatus*) from ADAS Boxworth and short and long dormancy winter barley stock supplied by East of Scotland College of Agriculture (ESCA).

The cultivation treatments were tine cultivation to 5 cm (Boxworth only); tine cultivation 10 cm; tine cultivation to 15 cm; plough to 15 cm and plough to 20 cm. The various cultivation treatments were repeated on the same plots for each of the three years.

All cultivations were done along the length of the plots. At Boxworth the tine cultivations to 5 cm and 10 cm were done with a pigtail tined cultivator and to 15 cm with a combined disc and heavy tine implement. Tine cultivation treatments were done at Bridgets with a light pigtail tined implement.

The primary cultivation treatments were done at Boxworth on 27-29 September 1988, 8 September 1989 and 11 September 1990 and the experiment was drilled on 7 October, 3 November and 11 October respectively. The ploughed treatments in autumns 1988 and 1989 had extra secondary cultivation treatments. At Bridgets the primary cultivations were on 11 October 1988, 21 August 1989 and 13 September 1990 and the experiment was drilled on 16 October, 12 October and 26 March respectively. All treatments were rotary harrowed and rolled before drilling at both sites each year.

The seedrates were 170-180 kg per ha for spring and winter wheat and row width was 12.5 cm at both sites.

Glyphosate was applied at recommended rates pre-harvest in 1988, to regrowth in July 1989 following the early removal of the crop and weed material, and to the stubble in July

1990. The trial areas were harvested with a combine harvester without taking yields along the length of the plots in 1990 and 1991 and the straw was burnt in both years. Fertiliser application and crop protection against broad-leaved weeds, disease and pests were in accordance with good farm practice.

At Boxworth, assessments of plant numbers from which percentage emergence was calculated were done using four quadrats per plot measuring 0.15 m x 0.15 m in autumn 1988 and subsequently all plants were counted on the whole of each sub-plot. At Bridgets, assessments were done in each plot on two fixed quadrats measuring 0.3 m x 0.3 m. At both sites each brome and barley plant was hand rogued as it was counted when the bromes were at the early panicle development stage in 1990 and 1991.

A very large flush of brome plants at both sites in the autumn in which seed was broadcast (1988), particularly with the tine cultivation treatments, was an impediment to the assessment in November of that year. Following tillering the weeds became so abundant, tangled and lodged that a further assessment could not be made in that cropping year. The crops were mown in June 1989 and removed by baling at Boxworth and by picking up with a forage harvester at Bridgets to prevent seed return.

RESULTS

The percentage emergence of seeds in the period November 1988-June 1991 are given in Tables 1 and 2. By far the greatest emergence of all species occurred in the autumn in which they were 'sown'. No barley survived to June of the second cropping year.

Levels of emergence of meadow brome were similar to barren brome each year at both Boxworth and Bridgets (Tables 1 and 2).

At Boxworth, differences in percentage emergence in November 1988 were significant ($P = 0.001$) between the ploughing and cultivation treatments; the differences were greater with the non-indigenous barren brome and both winter barley species. At Bridgets, there was significantly less emergence ($P = 0.001$) with the ploughed treatments over all species in November 1988.

There was no consistency in the differences in emergence with the different depths of tine cultivation. However, both ploughing treatments were more effective in reducing emergence (below 5 per cent) at both sites; the greater depth of ploughing usually resulted in a reduction in emergence in the first year. Levels of emergence in the two subsequent years were less than 0.05 per cent with tine cultivations and nearly always zero with ploughing at Boxworth and less than 0.2 per cent and 0.1 per cent with tines and ploughing respectively at Bridgets.

At Boxworth, very low levels of emergence of brome and barley had occurred at the assessment in October 1989 which was between the cultivation treatments being applied and drilling the winter wheat crop. Emergence of brome and barley following drilling of wheat in autumn 1989 and 1990 was so low that assessments were delayed until the following June in both years.

Table 1. Percentage emergence of seeds sown in autumn 1988, at ADAS Boxworth.

	Month and year of assessment			
Weed species and cultivation	Nov. 1988	Oct. 1989	June 1990	June 1991
Indigenous barren brome (*Bromus sterilis*)				
Tine, 5 cm	30	0.04	<0.01	<0.01
Tine, 10 cm	36	0.02	<0.01	0
Tine, 15 cm	26	0.02	<0.01	0
Plough, 15 cm	4	0	0	0
Plough, 20 cm	1	0	0	0
Non-indigenous barren brome (*Bromus sterilis*)				
Tine, 5 cm	41	<0.01	0	<0.01
Tine, 10 cm	43	<0.01	0	0
Tine, 15 cm	43	0	0	<0.01
Plough, 15 cm	1	0	0	0
Plough, 20 cm	1	0	0	0
Meadow brome (*Bromus commutatus*)				
Tine, 5 cm	34	0.01	<0.01	<0.01
Tine, 10 cm	34	0.01	0	<0.01
Tine, 15 cm	30	0.01	<0.01	<0.01
Plough, 15 cm	5	0	0	0
Plough, 20 cm	3	0	0	0
Winter barley, (cv Magie) short dormancy				
Tine, 5 cm	100	0.06	0	0
Tine, 10 cm	81	0	0	0
Tine, 15 cm	77	0.01	0	0
Plough, 15 cm	0	0	0	0
Plough, 20 cm	0	0	0	0
Winter barley, (cv Magie) long dormancy				
Tine, 5 cm	99	0.04	0	0
Tine, 10 cm	79	0	0	0
Tine, 15 cm	63	0	0	0
Plough, 15 cm	14	0	0	0
Plough, 20 cm	4	0	0	0
SED (59 DF)	9.99			

No plants of brome or barley had emerged at Bridgets between cultivation and drilling in autumn 1989. Only very low levels of barley and no brome were found when the site was assessed on 21 February 1990 and very few brome plants were present in July of that year. A stale seedbed produced in autumn 1990 encouraged a few brome seeds to germinate by January 1991 but no additional weeds were evident prior to sowing spring wheat in March 1991. Very low levels of both brome species were recorded in June 1991.

Table 2. Percentage emergence of seeds sown in autumn 1988, at ADAS Bridgets.

	Month and year of assessment				
Weed species and cultivation	Nov. 1988	Feb. 1990	Jul. 1990	Jan. 1991	Jun 1991
Indigenous barren brome (*Bromus sterilis*)					
Tine, 10 cm	29	0	<0.01	0.1	<0.01
Tine, 15 cm	30	0	<0.1	0.2	<0.01
Plough, 15 cm	4	0	0	0	0
Plough, 20 cm	1	0	<0.01	0	0
Meadow brome (*Bromus commutatus*)					
Tine, 10 cm	33	0	0	0.02	<0.01
Tine, 15 cm	26	0	<0.1	0.1	<0.01
Plough, 15 cm	3	0	<0.1	0	0
Plough, 20 cm	1	0	<0.01	0	0
Winter barley, (cv Magie) short dormancy					
Tine, 10 cm	44	0	0	0	0
Tine, 15 cm	53	0	0	0	0
Plough, 15 cm	13	<0.1	0	0	0
Plough, 20 cm	17	0	0	0	0
Winter barley, (cv Magie) long dormancy					
Tine, 10 cm	54	0	0	0	0
Tine, 15 cm	60	0	0	0	0
Plough, 15 cm	16	<0.1	0	0	0
Plough, 20 cm	5	0	0	0	0
SED (24 DF)	11.3				

DISCUSSION

Differences in levels of germination of seed on the soil surface have been found between populations of barren brome (Peters, 1990). The seed of the non-indigenous barren brome appeared to emerge more than the indigenous stock following tined cultivation only in the autumn in which they were spread on the surface; no differences were apparent in the two subsequent years (Table 1).

The results suggest that the seeds of the brome species used in this experiment had some dormancy. A low proportion did survive beyond one year with tine cultivation, and even when ploughed to a depth of 15 cm or 20 cm and ploughed up again in the second year at Bridgets.

The application of glyphosate a month after the crop and weeds were cut and removed in June 1989 was necessary to prevent reseeding of regrowth of brome. This indicates a possible source of seed carry over in commercial crops and incomplete burial with ploughing would be another.

The levels of emergence of barley in years two and three, under the combination of cultivation and glyphosate application, were less than with brome even where the seed was ploughed up again, indicating that the stocks of barley used would not have produced a volunteer problem after the first year.

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COLONISATION FROM SOIL SEED BANKS : RESULTS FROM AN EXTENSIVE PIPELINE SURVEY

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ABSTRACT

There was considerable variation in seed bank size and composition in habitats along the North West Ethylene Pipeline route prior to construction. Seed bank size was a poor indicator of numbers of seedlings produced after construction. Results showed that grasses and forbs produced many more seedlings / 1000 germinable seeds than rushes or ericoids. Soil moisture and pH had a substantial influence on seedling production but nutrient status was relatively unimportant.

INTRODUCTION

In 1990, semi-natural vegetation sites along the 406 km route of Shell's North West Ethylene Pipeline (NWEP) from Grangemouth to Stanlow were surveyed to provide a baseline for reinstatement prescriptions. The work entailed vegetation description, assessment of seed banks, and chemical analysis of soils. The pipeline was completed in autumn 1991, and in early summer 1992, some sites were re-visited to record the extent of spontaneous colonisation. These sites had not yet been re-seeded, so seedlings should have originated from the seed bank or seed rain. In the time period between pipeline completion and final vegetation analysis, seed rain was assumed to be minimal, but the actual contribution of seeds from this source was not measured.

Pipeline construction started with the topsoil being stripped from a 20m wide fenced easement. A 1m wide trench was excavated, the pipe lowered into the trench, and finally, the trench was backfilled, first with subsoil and then the topsoil was replaced. The result was a fairly uniform width of harrowed topsoil which was almost devoid of surviving vegetation.

This paper describes the seed banks of different habitats along the NWEP and colonisation of the easement a year after construction. It examines how far colonisation may have been affected by seed bank size or composition, and by site characteristics such as wetness, pH or soil fertility.

METHODS

During 1990, over a hundred sites of nature conservation, recreation or amenity interest were surveyed on the pipeline route. Vegetation species composition was recorded along selected permanent transects across the easement. Soil cores were taken for seed bank analysis (five bulked random cores 10 cm deep and 5 cm in diameter), and subsamples were used for soil analysis to provide data on pH and total phosphorus and potassium.

To determine seed bank size, the soil samples were dried at 25-30°C for 48 hours and passed through a 5mm mesh sieve to remove stones. A sub-sample of 100 ml was spread thinly over capillary matting and kept moist in a warm (6-25°C) greenhouse. The soils were stirred periodically to ensure as many seeds as possible were exposed to light. The trays were observed for six weeks, with seedlings categorised into grasses, rushes, forbs or ericoids. Using this technique, seeds can still appear after more than a year, although the largest numbers are usually recorded in the first few months. The six week period used here provided a minimal estimate, but nevertheless gave a reasonable comparison of relative numbers of seeds in different types of site.

In 1992, about half the sites were re-visited, those chosen provided a wide range of seed bank types and sizes. Sites already reinstated were discarded, and the final selection consisted of forty one sites. The species composition and number of seedlings were noted in five random quadrats (each 32 x 32 cm) at the locations used in the pre-construction survey. Soil moisture was assessed on a subjective scale of one to five (1- standing water, 2- wet, 3- moist, 4- damp, 5- dry).

RESULTS

The vegetation communities present prior to pipeline construction were classified into 22 groups. A summary of the vegetation groups, the nearest equivalent National Vegetation Classification types, seed bank size and nutrient status is given in Table 1. Nearly all the soil samples were deficient to some extent in P or K, and the Table shows vegetation types where severe deficiencies were frequently noted (P= 0-7 ppm, K =0-45 ppm). There was wide variation in the number of germinable seeds in the seed banks (from 2,000 to >1,000,000 m^2). The seed bank size varied considerably with the vegetation, but there was also great variation from site to site within the same vegetation type. The smallest seed banks (mean < 50 k/m^2) were found under *Eriophorum* communities, tall herb grassland, herb rich meadows, bracken communities, neutral grassland and scrub. Densities of more than 150 k/m^2 were recorded in *Deschampsia cespitosa* grassland, rush, sedge and hedge communities. Overall, rushes were the most numerous seed category, with ericoids and forbs being intermediate and grasses the least numerous.

Not all the vegetation communities were sampled in the repeat survey. The main types were rush grassland (4 sites), *Nardus* grassland (6), acid grassland (5), other grasslands (8), *Calluna* heath (9) and others (9). The "others" group consisted of a range of sites, including *Eriophorum* bog and larch plantation. There were marked differences in the numbers of seedlings found at the various site types (Table 2).

Obvious features were the predominance of rush seedlings at rush grassland and of ericoid seedlings at the *Calluna* heath sites. The rush sites had on average more than three times as many seedlings as any of the other site types. However, although rush seedlings were found at virtually all sites, ericoid seedlings were mainly confined to *Calluna* sites.

Seedling density in relation to seed bank size

Overall, the correlation between total seed bank size and number of seedlings was poor ($R^2 = 0.13$) (Figure 1). An important contributory factor was the wide variation in the proportion of seedlings produced by the four main seed categories. Although rush grassland sites had the

Table 1. *Mean buried seed populations (thousand seeds/m^2) in habitats along the North West Ethylene Pipeline and nearest equivalent NVC equivalent community type; n = no.sites ; * = severe deficiency; t = trace.*

	NVC type	(n)	Grasses	Forbs	Rushes	Ericoids	Total	(range)	Deficiency: P	K	Mean pH
Tall herb (spp rich)	*	(5)	3	11	25	-	39	(23-138)	*	*	5.5
Tall herb (spp poor)	MG1	(5)	t	4	11	t	15	(2-39)			5.7
Herb rich meadows	MG5	(6)	5	20	4	-	29	(5-97)	*		5.9
Improved pastures	MG6	(14)	9	23	56	6	94	(2-457)	*	*	5.5
Neutral grassland	MG1	(7)	13	28	4	1	46	(13-119)		*	6.3
Deschampsia cespitosa grassland	U13	(4)	8	5	216	3	232	(45-273)	*		4.8
Nardus grassland	U5	(14)	3	2	72	22	99	(2-271)	*		4.1
Dry acid grasslands	U4	(10)	8	7	84	23	122	(19-404)	*		4.8
Wet acid grasslands	U4	(16)	4	17	63	12	96	(19-273)	*	*	4.5
Dry heaths	H9	(17)	t	21	3	65	89	(49-138)	*	*	4.5
Wet heaths	M21	(11)	3	3	11	42	59	(30-79)	*	*	3.9
Grassy heaths	U4	(7)	2	3	77	42	124	(21-414)	*		4.3
Eriophorum communities	M20	(8)	t	t	8	29	37	(2-154)	*	*	3.5
Rush communities	M13	(8)	14	9	333	14	370	(30-1290)	*		4.4
Sedge communities	U6	(4)	3	124	85	12	224	(2-504)	*	*	4.5
Sphagnum bogs	M19	(5)	1	t	58	52	111	(18-193)	*	*	4.0
Bracken communities	U20	(3)	1	27	7	6	41	(2-110)	*		5.4
Woodlands	W8	(21)	4	11	33	2	50	(2-216)	*		4.8
Hedges	MG1	(2)	9	14	148	-	171	(11-331)	*		6.0
Scrub	W25	(6)	8	8	21	-	37	(5-71)			5.9
Mean			5	17	66	17					

Table 2. *Numbers of seedlings/ m^2 in the six categories of site (n=number of sites).*

	(n)	Grasses	Rushes	Forbs	Ericoids	Total
Rush grassland	(4)	58	259	69	1	387
Nardus grassland	(6)	22	63	14	1	100
Acid grassland	(5)	77	16	50	1	144
Other grassland	(8)	60	38	48	0	146
Calluna heath	(9)	14	26	6	27	73
Others	(9)	44	18	69	0	131

largest number of seeds and seedlings per m^2, the seed banks produced proportionally few seedlings (0.5 seedlings / 1000 viable seeds). Only ericoid seed banks had lower productivity. In contrast, grass seed banks resulted in 16.5 seedlings / 1000 seeds, with forbs being intermediate, having a rate of 3.7 seedlings / 1000 seeds (Table 3).

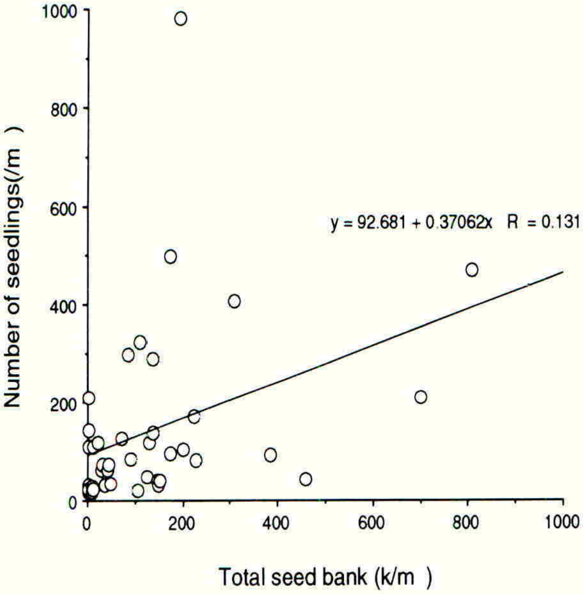

Figure 1. Relationship between total seed bank size and number of seedlings produced after construction.

Table 3. *Numbers of seedlings established / 1000 viable seeds in the seed bank.*

	Rushes	Grasses	Forbs	Ericoids
Mean seed bank size (1000/m^2)	104	2.6	11	19
Mean seedling density(/m^2)	53	43	41	6
Seedlings / 1000 seeds	0.5	16.5	3.7	0.3

Effects of soil moisture on the number of seedlings

There were substantial differences in the numbers of seedlings established in the site moisture categories. Rush seedlings were most numerous at wet sites, with absolute numbers minimal on the driest sites. Grass and forb seedling numbers were similar on all sites, as were ericoid seedlings on the three dampest categories, but ericoid seedlings were absent on the driest sites.

The numbers of seedlings / 1000 seeds was greatest on wetter sites for rushes, grasses and forbs, and figures tended to decline at drier sites. Ericoids peaked on moist soils (Table 4).

Table 4. *Numbers of seedlings established / 1000 viable seeds in the seed bank in the soil moisture categories (*, p<0.05; 10%, p<0.1)*

	Moisture category				
	2 (Wet)	3	4	5 (Dry)	p
Grasses	42.6	17.0	10.7	14.9	10%
Rushes	0.7	0.4	0.3	0.1	*
Forbs	12.9	5.0	6.6	0.9	*
Ericoids	0.2	1.3	0.2	0	*

Effects of pH

31 sites were acid, pH 3.5-4.9, 7 were intermediate, pH 5-6.6 and 3 were alkaline, pH 6.7-7.8. Absolute rush seedling numbers increased with soil acidity, whereas grass and forb seedlings peaked at neutral sites . Ericoid seedlings were only recorded on acid soils. The numbers of seedlings / 1000 seeds indicated that the germinability of the rush, ericoid and forb seed groups increased with soil acidity, whereas grasses established equally successfully in acid, neutral and alkaline soils (Table 5).

Table 5. *Proportions of seedlings established / 1000 viable seeds in the seed bank in each of the pH categories (*, p<0.05; ns, not significant).*

		pH category:		
	Acid	Neutral	Alkaline	p
Grasses	17.3	14.8	22.0	ns
Rushes	0.5	0.4	0.02	*
Forbs	8.1	3.4	0.5	*
Ericoids	0.3	0	0	*

Effects of nutrient status

Sites were divided into those with severe deficiency in either P or K (or both) (35 sites) and those without such deficiency (6 sites). There were no significant differences between the size of the seed bank and the number of seedlings established, and the number of seedlings established / 1000 seeds in each seed category was similar regardless of nutrient status .

DISCUSSION

Seed bank size was very variable between vegetation types and also within sets of similar sites, but the size of the seed bank had little bearing on the number or species of seedlings recruited after disturbance, in line with the findings of Grime *et al* 1988; Freedman *et al* 1982.

Although grasses formed the smallest seed banks, their proportional germination was high. Many common grasses form transient seed banks in the soil which remain viable for less than twelve months (Thompson and Grime, 1979). This accounts for the small seed banks found in this group. The forbs had the next highest germinability, many being in a second transient seed group where winter dormancy is followed by germination in the early spring (Froud-Williams *et al* 1984).

Rush and ericoid seeds are small in size, most require light to germinate, and form persistent seed banks (Thompson and Grime, 1979). Seeds must be close to the soil surface for germination to take place, and hence are prone to desiccation. Their low proportional germination probably reflects the relatively small number of seeds actually at the surface, the high desiccation risk, and the limited carbohydrate reserves of small seeds (Oberbauer *et al*, 1982; Hegarty *et al*, 1978).

Both decreasing soil moisture and acidity appeared to be factors limiting the recruitment of rush, forb and ericoid seeds. Oberbauer and Miller (1982) found most species require nearly saturated soils for germination and seedling establishment. However, the largest seed banks often occur where soil conditions are acid and / or waterlogged (Harper,1977). These conditions may be favourable for seed storage, but may also be advantageous for seedling production when the ground is disturbed and vegetation cover is removed.

Nutrient status did not affect seedling recruitment from any of the seed groups, but may be an important factor in maintaining seedling development.

This study shows that seed bank size is not a good guide to the likely number of seedlings established after disturbance. The proportions of the main seed types give an indication of potential seedling composition, but numbers are considerably influenced by soil wetness and acidity. On the NWEP a combination of moist or wet, slightly acidic conditions tended to produce the largest number of seedlings. Using this information would be difficult in practice, since most reinstatement also involves seeding and fertilising. Nevertheless, the results give some insight into the factors influencing the potential numbers of seedlings that might establish following disturbance of different types of soil seed bank.

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THE IMPLICATIONS OF THE ANNUAL DORMANCY CYCLE OF BURIED WEED SEEDS FOR NOVEL METHODS OF WEED CONTROL

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ABSTRACT

This paper describes the annual dormancy cycles of seeds of *Avena fatua, Chenopodium album* and *Rumex crispus* buried in soil. We aimed to identify (1) times when dormancy is low and the environmental stimulus to germination is high and (2) the ability of dormancy-relieving chemicals to stimulate germination at such times. Seeds were buried in soil at various depths and recovered after different periods. Retrieved seeds were germinated with and without chemicals at temperatures similar to those in the field at retrieval. Dormancy of *A. fatua* seeds was relieved in the autumn and enforced in late spring. By contrast, dormancy of both *C. album* and *R. crispus* was relieved in the spring and enforced in the autumn. Chemical treatments enhanced the germination of all three species when seeds were recovered at times of low dormancy. The implications for using chemical seed treatments in the field are discussed.

INTRODUCTION

Most weed infestations arise from seeds in the soil. The "successful" weed seed must be in the right physiological state to germinate in the right place, usually within a limited period.

Weeds can seldom satisfy these requirements if seeds germinate as soon as they are shed. Instead seeds may remain for long periods in the soil seed bank with intermittent germination of a part of the population. If seeds are to survive in the soil, viability must be maintained for as long as germination is avoided by dormancy or quiescence. Dormancy is a failure to germinate given moisture, air and a suitable constant temperature for radicle emergence and seedling growth. If these minimum requirements for germination are lacking the seed is quiescent since metabolism will often be reduced. Longevity of imbibed seeds depends upon the dormancy present at shedding either not being lost or being reinforced during burial. Harper (1957) introduced the terms innate, induced and enforced dormancy to describe dormancy which develops on the mother plant, dormancy which is induced after shedding and dormancy which is enforced by unsuitable environmental conditions, respectively.

In many species, innate dormancy prevents seed germination on the mother plant and immediately after shedding. The rate of loss of innate dormancy in air-dry seeds increases with temperature. On a bare soil surface, innate dormancy may decrease rapidly as seeds may be warmer and drier than under a crop canopy or in a hedgerow (Murdoch & Ellis, 1992).

Dormancy may be induced in both dormant and non-dormant seeds after shedding. It is induced very rapidly in anaerobic atmospheres and more slowly in moist aerobic conditions like those

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found in soil. The rate of induction of dormancy in imbibed *Rumex crispus* seeds increases with temperature (Totterdell & Roberts, 1979).

Buried seeds which fail to germinate *in situ*, often germinate when soil is spread out in thin layers or when seeds are brought to the soil surface. Harper (1957) originally explained this as dormancy enforced by depletion of oxygen or surfeit of carbon dioxide. More recently, the darkness and reduced temperature fluctuations experienced by buried seeds have been shown to be more important. Further examples of enforced dormancy are the inhibition of germination caused by prolonged exposure to white light especially at high radiant flux densities as might occur on a bare soil surface or to far-red light, for example, under a leaf canopy (Murdoch & Ellis, 1992). This change in interpretation of enforced dormancy to include light and fluctuating temperatures, implies that we are often dealing with innate and/or induced dormancy. It is, however, useful to have a term such as enforced dormancy to identify factors in the environment which prevent germination *in situ* at any given time where the dormancy might be relieved by, for example, bringing seeds to the soil surface.

When seeds are shed to the soil, variation in the degree of dormancy among the seeds, provides both the potential for considerable persistence in extreme individuals, and a regular proportion of (surviving) seeds which germinate each year. This annual emergence depends on an interaction of the soil environment and the dormancy of seeds buried in the soil.

Annual cycles in which dormancy of seeds in soil is relieved and induced during the course of a year were first described by Courtney (1968) for *Polygonum aviculare* and they have since been shown for many other temperate and tropical species (Baskin & Baskin, 1985; Garwood, 1989). The annual dormancy cycle of *Avena fatua* seeds in soil near Reading in the south of England is presented in detail and similar cycles are described for *Chenopodium album* and *R. crispus*. These cycles are discussed with respect to the potential use of chemicals to relieve the dormancy of buried weed seeds, thereby achieving weed control by depletion of the soil seed bank.

MATERIALS AND METHODS

A. fatua florets (hereafter called seeds) were collected from infestations near Blewbury, Oxfordshire. Fruits of *C. album* L. and *R. crispus* L. were collected from Sonning and Lane End Farms respectively, near Reading, Berkshire. All seeds were dried to about 10% moisture content (wet weight basis), cleaned and stored at -20°C for up to four months before use. Seeds were buried at various depths in polyester mesh packets at Sonning Farm, Reading in a stoneless loamy coarse sandy soil with very free drainage. Three replicate packets were recovered at intervals to assess seed survival, germination and dormancy. In one experiment seeds were buried at depths of 25, 75 and 230 mm on 27-28 December 1974 (c. 1200 seeds/packet) and recovered over 3.25 years. Germination treatments on retrieved seeds included darkness and light, water and 10 mM potassium nitrate and different temperatures. In a further experiment, seeds were buried at depths of 10 and 100 mm on 7 August 1989 (400 seeds/packet) and were recovered at the dates shown in Table 1 to monitor potential responses of seeds near the soil surface to a dormancy-relieving chemical cocktail comprising 10 mM potassium nitrate, 6.5 mM thiourea, 0.7 mM 2-(chloroethyl) phosphonic acid (as "Cerone"), 1.0 mM sodium azide and 0.1 mM hydrogen peroxide. These seeds were germinated in darkness at alternating temperatures approximating those in the soil at retrieval. The upper and lower temperatures of the alternating temperature regimes were the mean minimum and maximum daily soil temperatures at 10 mm depth for six days prior to each retrieval date (Table 1). The time spent at the upper temperature of the alternation (the thermoperiod), was the average time per day spent above the mid-temperature over the six-day period, the mid-temperature for a given day being the average of the soil minimum and maximum temperatures. Germination results are expressed as mean percentages of the initial number of seeds at burial.

TABLE 1. Mean minimum and maximum daily soil temperatures (°C) and thermoperiods (in hours and minutes) at a depth of 10 mm for six days prior to each retrieval date.

Retrieval date	Temperature min.	Temperature max.	Thermo-period	Retrieval date	Temperature min.	Temperature max.	Thermo-period
18/ 09/ 89	13.0	19.0	9:30	20/ 08/ 90	16.9	33.6	10:00
30/ 10/ 89	4.5	11.5	10:00	01/ 10/ 90	9.0	21.0	10:00
11/ 12/ 89	-3.6	1.9	10:00	12/ 11/ 90	2.8	11.4	7:00
22/ 01/ 90	1.9	7.7	10:00	24/ 12/ 90	1.0	4.2	8:30
05/ 03/ 90	1.2	8.2	10:00	04/ 02/ 91	0.1	2.1	7:00
04/ 05/ 90	11.3	30.5	11:00	18/ 03/ 91	6.2	14.5	9:00
28/ 05/ 90	10.5	29.5	10:30	29/ 04/ 91	2.7	19.0	9:30
07/ 07/ 90	12.9	27.7	8:00	10/ 06/ 91	11.6	18.1	9:30

RESULTS

Dormancy of *A. fatua* seeds in soil increased rapidly after burial such that all surviving seeds were fully dormant after three months in the soil (Figure 1). In many seeds, this dormancy could not even be overcome by 10^{-2} M gibberellic acid (GA_3; data not shown). Most seeds retrieved between March and October remained fully dormant (Figure 1) even though the depth of this dormancy decreased slightly in midsummer. During the autumn the depth of dormancy declined rapidly although most seeds were still technically dormant. It was, however, an enforced dormancy which could be relieved by low temperatures and nitrate. A slight decline in the germination of retrieved seeds at 3°C between January and March 1976 can be explained by *in situ* germination at this time (Figure 1). Thereafter, *in situ* germination virtually ceased and a deeper physiological dormancy was induced in most seeds (Figure 1). Low temperatures and nitrate could not relieve this deeper dormancy. This induction of dormancy in late spring followed by loss of dormancy in autumn recurred into the third year of burial and qualitatively similar results were obtained for seeds buried at depths of 25 and 75 mm (data not shown).

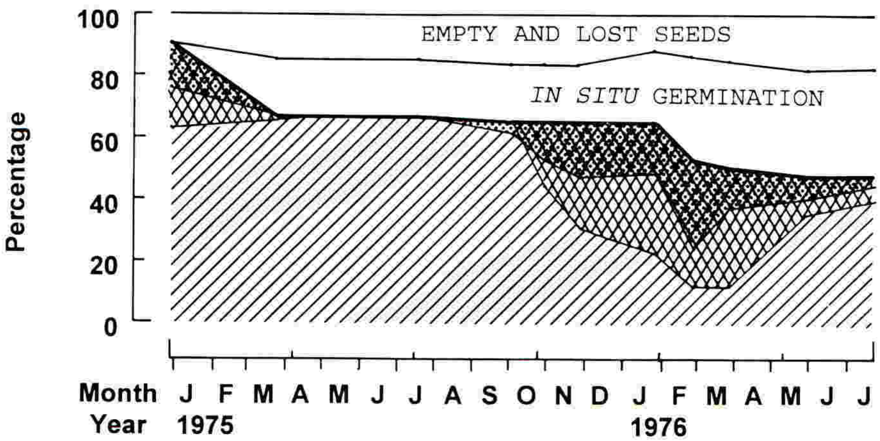

FIGURE 1. Seasonal variation of dormancy and germination of seeds of *Avena fatua* recovered from a depth of 230 mm in soil. Germination was tested in darkness in 10 mM potassium nitrate. Key: ▩ retrieved seeds germinating at 10°C; ▒ retrieved seeds germinating at 3°C; ▨ deeply dormant viable seeds.

In the second experiment, germination of retrieved *A. fatua* seeds was again markedly higher during autumn and from late winter to early spring (Figure 2), but no germination was observed at December retrievals when the mean maximum soil temperature was only 1.9°C (Table 1). The dormancy-relieving chemical mixture was most effective when the seeds were more responsive and the temperatures were suitable, i.e. in autumn and spring for *A. fatua* (Figure 2). The effect of this mixture in *A. fatua* was more pronounced in the more dormant seeds retrieved during the first year of burial.

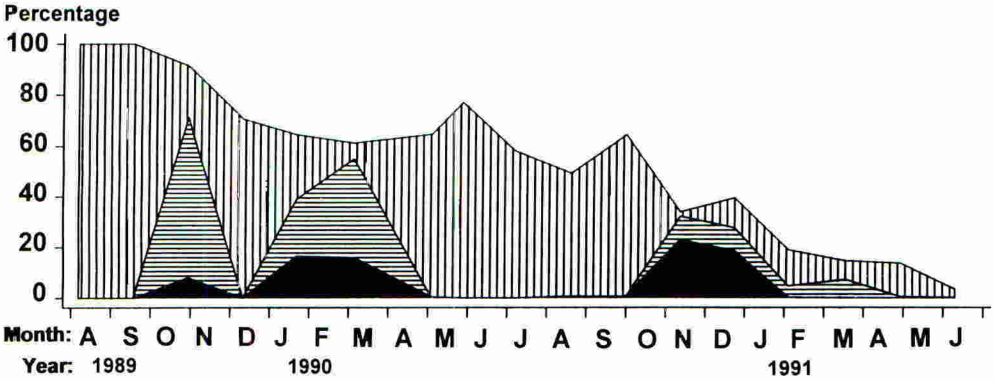

FIGURE 2. Seasonal variation in the effect of dormancy-relieving chemicals of seeds of *Avena fatua* retrieved from 10 mm depth of soil. Germination tests were carried out at temperatures similar to those in the soil before retrieval (Table 1). Key: retrieved seeds capable of germinating in 1 mM potassium nitrate █ (a typical concentration in the soil in the experimental site); additional germination in a dormancy-relieving chemical mixture ▤ and viable seeds in deep dormancy which failed to germinate in tests ▥ .

In principle, similar effects were obtained for *C. album* and *R. crispus* but, unlike *A. fatua*, dormancy of these species was relieved in the spring and enforced in the autumn and the chemical cocktail had most effect on seeds recovered between spring and autumn (data not shown). Seeds were also buried at 100 mm depth but the difference of environment compared to 10 mm (Figure 2) had little effect on percentage seed germination in chemicals. The environment at 10 cm was, however, more suitable for dormancy release in *A. fatua* (data not shown).

DISCUSSION

Germination of seeds in the field occurs at times of low or no dormancy if sufficient moisture is available and temperatures are suitable for germination. These responses help to explain the periodicity of seedling emergence which characterises many species. The results presented show chemical treatments could increase the proportion of seeds germinating at these times of low dormancy by relieving residual innate and induced dormancy. It is, however, particularly striking that the seasonal periodicity of germination was not circumvented by the dormancy-relieving chemical mixture being tested. For all three species, the ideal time to apply dormancy-relieving chemicals to buried seeds corresponded to the period when dormancy was least and soil temperatures most promotive.

Implications for weed control via the soil seed bank

Since the cause of most weed problems is the seed bank in the soil, weed scientists have long wondered whether it would be practicable to target the seed bank rather than the infestation. Typical depletion rates of the persistent seed banks of common weeds vary from 15 to 60% per annum depending on species and frequency of cultivation (Roberts & Dawkins, 1967; Roberts & Feast, 1973). Even if the rate of depletion consistently exceeded 80%, however, about seven years would be required for a seed bank to decrease by a factor of 10^5, for example, from 1000 seeds m^{-2} to 100 ha^{-1} (Figure 3). Were such depletion achieved in a single year by chemically relieving seed dormancy, weeds would not be eliminated; but the need for weed control in a following crop may be obviated or the containment of infestations using low doses of herbicides may become more practical.

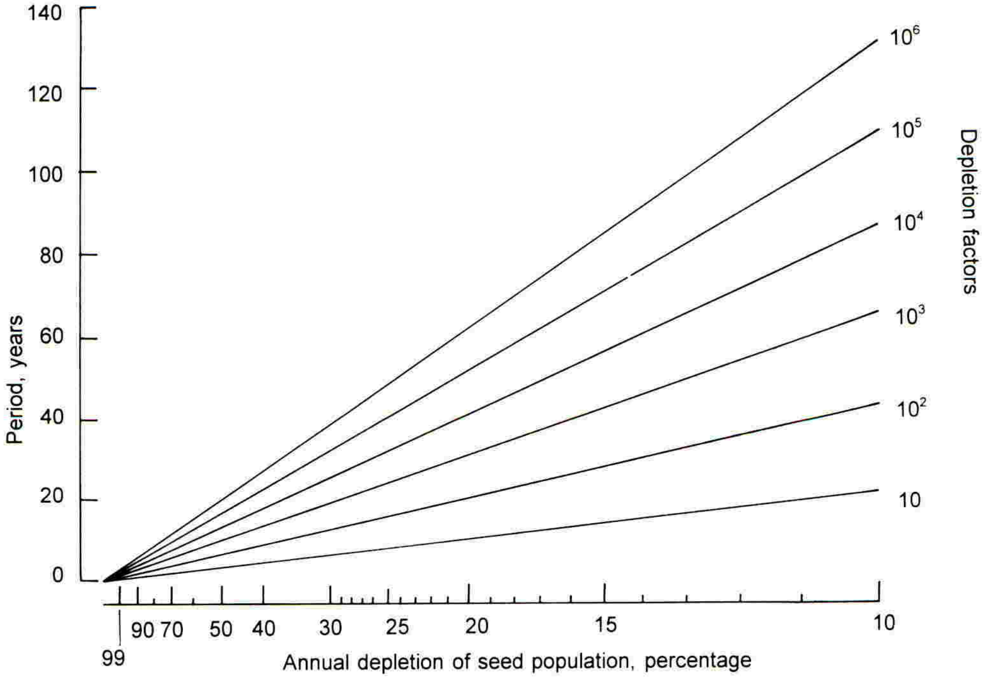

FIGURE 3. The time required to deplete soil seed banks by factors of ten to one million (10 to 10^6 shown against each line) as a function of an assumed constant annual rate of depletion. The depletion factor is the ratio of the initial to the final seed population (After Murdoch & Ellis, 1992).

Attempts to deplete seed banks by stimulating seeds to germinate have given insufficiently reproducible results for commercial application (Fay *et al.*, 1980; Thomas 1989; Bond & Burch 1990; Peters & West 1991). The results presented show that cultural and chemical treatments designed to deplete weed seed banks in the soil by stimulating the germination of dormant seeds are unlikely to succeed or to be reproducible unless care is taken to ensure that soil temperatures are promotive and seed dormancy is at low levels. Other factors may also influence the success of dormancy-relieving treatments. Soil moisture, nitrate and pH may influence the extent to which dormancy and quiescence are enforced. Similarly, vegetation cover and cultivation will alter the exposure of seeds to light and temperature fluctuation.

The chemicals are also important. Most applications of chemicals to the soil seed bank to date have employed single chemical treatments such as nitrate, azide, gibberellin or ethylene. The use of mixtures may, however, widen the range of species affected and expose a synergism. Optimal concentrations of chemicals for relief of dormancy are also usually lower in mixtures than when applied alone. Perhaps the greatest problem is to ensure that buried seeds experience promotive concentrations of chemicals. Rates of diffusion and degradation must therefore be considered since chemicals such as those in the dormancy-relieving cocktail tested in this paper are selected partly because of their short persistence in soil.

Only given such precautions will it be possible to test the hypothesis that rapid depletion will ensue if a dormancy-relieving chemical mixture is applied to the soil at a time of the year when seeds are at a low level of dormancy in their annual dormancy cycle and when soil temperature and moisture are suitable for germination of seeds of target species.

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