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INFLUENCE OF CULTIVATION REGIME UPON BURIED WEED SEEDS IN ARABLE CROPPING SYSTEMS

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SUMMARY

- (1) The effects of cultivation on the number of seeds of different species in arable land were investigated at four sites over several years. Soil cores were obtained from uncultivated and ploughed plots, and the seed content determined by germinating the seeds and counting and identifying the emerged seedlings.
- (2) Distribution of seeds was not uniform in the soil profile, and fluctuated annually on ploughed plots. Seed decline, although not markedly different between treatments, was more rapid in ploughed soil. The rate of seed decline at different depths was similar for both uncultivated and ploughed plots. Successful germination alone could not account for the rate of seed decline reported, indicating that losses from other causes were substantial.
- (3) A considerable number of species were recorded in the seed bank (23-30), but only a few (3-4) comprised the majority. A number of species present in the seed bank of uncultivated soil were absent from the seedling flora.

INTRODUCTION

The influence of different cultivation regimes upon the seedling weed flora of cereal rotations has been extensively investigated (Bachthaler 1974; Jan, Fontaine & Dumont 1976; Pollard & Cussans 1976, 1981; Cussans et al. 1979; Froud-Williams, Drennan & Chancellor 1983), yet few studies have been made of their influence on the number and distribution of buried weed seeds. A study of weed seeds in the soil is essential for a complete study of the effects of changing cultural practice on weed populations, for the seed bank may be considered to be an extension of the weed flora (Major & Pyott 1966). Any modification of the actual flora will bring about a modification of this potential flora, but in view of the magnitude of the seed bank, these changes may be slow (Beuret 1980).

Numbers of weed seeds in arable soils may be considerable, ranging from 1000 m^{-2} to $20\ 000\ \text{m}^{-2}$ (Kropáč 1966) and as high as 496 000 m⁻² (Jensen 1969). In a survey of buried weed seeds of cereal fields, between 1800 and 67 000 viable seeds m⁻² have been reported (Lockett & Roberts 1977).

Factors affecting demography of buried seeds have been discussed by Cook (1980) and the effects of cultural practice on seed banks have been considered in a recent review (Roberts 1981).

Whilst it is maintained that distribution of seeds in arable fields is relatively uniform throughout the working depth (Kropáč 1966), much of the evidence is to the contrary. For example, ploughing to a depth of 20 cm resulted in an uneven distribution of seed (Soriano et al. 1968). Roberts (1963a) reports that deep ploughing (36-41 cm) decreased seed density in the upper 15 cm but increased density below this depth, whereas shallow ploughing (15-18 cm) had the converse effect. He concluded that continued deep cultivation resulted in a more even distribution of seed with depth, although slightly more

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seeds were present at depths between 15 and 30 cm. He also states that the distribution with depth does depend very much upon when the soil is examined in relation to cultivations and seed production by the weeds (Roberts 1970).

In studies where seed return has been prevented, seed decline varied little between the various types of primary cultivation (Russell & Mehta 1938; Roberts 1963a, b; Roberts & Stokes 1965). However, seed decline may be less rapid in the absence of cultivation (Roberts & Dawkins 1967; Roberts & Feast 1973a). For uncultivated soil, losses of seeds at different depths will be disproportionate, with a greater rate of decline from the surface horizon, provided that seed return is prevented (Jan *et al.* 1976; Fourbet, Huer & Jan 1977).

This paper presents results on the effects of no-cultivation or ploughing on the seed banks of four experimental sites under arable crop rotations, and forms part of a larger study on the influence of cultivations upon weed flora composition (Froud-Williams *et al.* 1983).

MATERIALS AND METHODS

Soil cores (25 mm in diameter \times 200 mm deep) were taken from uncultivated and from ploughed plots over a period of three consecutive years at four experimental sites in Berkshire and Oxfordshire. These experiments were designed primarily to investigate the effects of cultivation regime on soil conditions and crop growth and began 3 years before these studies commenced. Arable crops were grown in rotation at three of the sites, Englefield, Northfield and Compton Beauchamp, whereas successive crops of winter wheat were grown at Compton. Crops were direct-drilled into uncultivated plots and conventionally sown on cultivated plots after ploughing to a depth of 20 cm. Plots measured 26×42 m at the former three sites and 16×32 m at Compton. Details of the sites and herbicide use are given elsewhere (Froud-Williams *et al.* 1983). The best available methods of weed control were applied to all plots. Seeds were largely prevented from shedding within the plot area but failure to control grass weeds adequately in 1978 resulted in further seed return at both Compton Beauchamp and Northfield.

Twelve cores were obtained per plot, by sampling at intervals of 7 m along a transect 10 m from the edge of the plot. The positions were fixed in order to obtain subsequent samplings within 15 cm of the original position. Samples were taken in spring to minimize differences in weight of soil which could have resulted from lower soil bulk density in autumn on ploughed plots. Any cores which were obviously compacted or contained large quantities of flint were discarded.

Cores were sectioned into four 50 mm layers and the same layers from all twelve cores were bulked. The soil was crumbled and mixed with an equal volume of a peat/sand mixture (3:2 v/v), and transferred to earthenware pans and kept regularly watered in an unheated glasshouse. Seed germination was encouraged by stirring the soil at monthly intervals in the year of collection but only every 3 months in subsequent years. Emerged seedlings were identified, counted and removed before each stirring. Samples were maintained for a period of 2 years. Plant names follow Clapham, Tutin & Warburg (1962).

RESULTS

The numbers of seedlings which emerged from the soil cores extracted over the 3-year period are given in Table 1. The majority of emergence occurred in the year of sampling with only 4-11% further emergence after the first year and very little after 18 months.

		No		
Site	Year	cultivation	Plough	S.E. ±
D 1011	(1977	5262	3563	117
Englefield SU 615698	{ 1978	2622	1332	97
	l 1979	1748	832	69
Northfield SU 339911	(1977	4995	2762	133
	{ 1978	2706	1415	119
	(1979	1998	1082	71
	(1977	4129	4096	96
Compton Beauchamp SU 272876	₹ 1978	1965	1132	71
	1979 ا	2497	932	122
Compton*	(1977	1124	2289	80
SÛ 512791	(1978	792	1331	31

TABLE 1. Total estimated seed density at the four sites (seeds m⁻²)

Germination after 18 months was restricted to a few species which either show marked periodicity of germination, e.g. *Polygonum aviculare*, or have protracted dormancy, e.g. *Papaver rhoeas*.

The mean total seed banks at Northfield, Compton Beauchamp and Englefield were very similar (3879, 4113 and 4413 seeds m⁻² respectively) with greater numbers of seeds on uncultivated than on ploughed plots in all years. However, at Compton there were fewer seeds in the soil (1707 m⁻²) but more seeds on ploughed than uncultivated plots. As the seedling emergence technique was used, the data refer to germinable seeds and not total seeds or total viable seed and is presumably an underestimate of the buried seed bank.

Seeds were unevenly distributed between depth horizons (Fig. 1). Samples collected from Englefield and Northfield in 1977 had most seeds in the 100–150 mm horizon irrespective of cultivation treatment. In 1978 and 1979 a similar distribution occurred for uncultivated plots only. At Englefield the majority of the seed population was present in the 50–100 mm horizon of ploughed plots in 1978 whereas density was greater in the 100–150 mm horizon in 1979. At Compton greatest numbers of seeds were located in the 150–200 mm and to a lesser extent 0–50 mm horizons of uncultivated plots in both 1977 and 1978. On ploughed plots most seeds were in the 50–100 mm horizon in 1977 but in the following year density was higher in the 100–150 mm horizon.

The rate of seed decline was determined by calculating the difference in seed numbers between years and expressing the results as a percentage of the total seed burden present in 1977. Seed decline was more rapid in ploughed plots than uncultivated ones, although percentage decline varied between sites and at Northfield there was little difference between treatments (Table 2).

The composition of the seed bank differed considerably from that of the seedling flora on uncultivated plots, but was more comparable on ploughed plots. Species infrequent as seedlings were often present in the seed bank. Examples include *P. aviculare* on uncultivated plots and *Alopecurus myosuroides* on ploughed plots. Conversely, species absent from the seed bank were occasionally present as seedlings, e.g. *Epilobium* spp. and *Sonchus* spp. Details of the seedling flora are presented in a previous paper (Froud-Williams *et al.* 1983).

The actual weed flora was often much less than 1% of the potential (Table 3). For example, actual and potential weed floras at Englefield in 1977 were 17 and 5262 m⁻² without cultivation, and 68 and 3563 m⁻² with cultivation. Another difference between actual and potential weed floras was the paucity of perennial species in the former.

^{*} Experiment terminated autumn 1978.

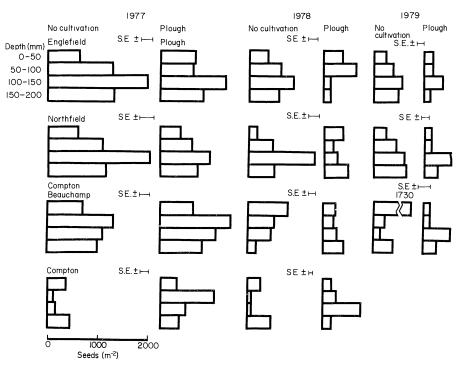


Fig. 1. Effect of cultivation on distribution of seeds in the soil profile. S.E., standard error of the interaction between cultivation and depth.

TABLE 2. Rate of seed decline (expressed as % of 1977 seed bank)

	No	*	
Year	cultivation	Plough	
(1977–1978	50.2	62.6	
(1977–1979	66.8	76∙6	
(1977-1978	46.0	49.0	
(1977–1979	60.0	60⋅2	
(1977–1978	52.4	72.4	
1977-1979	39.5*	77.2	
1977–1978	29.6	41.8	
	(1977–1978 (1977–1979 (1977–1978 (1977–1979 (1977–1978 (1977–1979	(1977–1978 50·2 (1977–1979 66·8 (1977–1978 46·0 (1977–1979 60·0 (1977–1978 52·4 (1977–1979 39·5*	

^{*} Seed return not prevented.

TABLE 3. Actual weed flora recorded in April expressed as a percentage of the potential flora

Site	Year	No cultivation	Plough
	(1977	0.3	1.9
Englefield	{ 1978	0.4	2.3
	l 1979	1.3	3.5
	(1977	0.3	0.8
Northfield .	₹ 1978	0.4	1.9
	1979	0.9	1.4
	(1977	1.0	0.5
Compton Beauchamp	₹ 1978	$1 \cdot 7$	2.9
•	1979 ا	1.6	0.3

TABLE 4. Percentage contribution of annual and perennial species to the seed bank

			Grass weeds		Dicotyledonous weeds	
Site	Treatment	Year	Annual	Perennial	Annual	Perennial
Englefield	No cultivation	1977–1979	8	12	78	2
	\ Plough	1977–1979	6	6	86	2
Northfield	∫No cultivation	1977–1979	39	6	53	2
	\Plough	1977–1979	22	3	70	5
Compton Beauchamp	No cultivation	1977–1979	55	3	35	7
	Plough	1977–1979	35	0	61	4
Compton	No cultivation	1977-1978	17	0	82	1
	\Plough	1977–1978	38	0	62	0

TABLE 5. Number of species in seed bank

Site	Year	No cultivation	Plough	Total number of species
	(1977	24	20	30
Englefield	{ 1978	13	10	14
	(1979	14	7	17
	(1977	14	19	23
Northfield	{ 1978	10	7	12
	l 1979	11	8	12
	(1977	15	18	23
Compton Beauchamp	{ 1978	11	9	12
	1979	13	9	15

TABLE 6. Number of seeds/60 cm² soil

		No cultivation			Plough		
Site	Dominant species	1977	1978	1979	1977	1978	1979
Englefield	Polygonum aviculare	29	26	17	14	6	9
•	Agrostis gigantea	29	0	0	17	0	0
	Viola arvensis	14	8	5	16 °	2	6
	Anagallis arvensis	13	8	7	14	11	3
	Other species	73	21	13	46	13	2
Northfield	Juncus bufonius	22	18	0	5	1	0
	Alopecurus myosuroides	32	12	6	12	3	2
	Polygonum aviculare	10	10	6	5	3	4
	Tripleurospermum maritimum	46	16	11	26	20	10
	Poa annua	6	4	12	2	0	0
	Other species	34	15	13	33	7	10
Compton	Juncus bufonius	46	13	3	22	5	1
Beauchamp	Poa annua	22	14	45	25	11	4
	Stellaria media	14	9	8	5	0	0
	Plantago major	16	5	6	49	12	18
	Other species	26	18	13	22	6	5

The majority of species represented in the seed banks were annuals (Table 4). Numbers of species recorded in the seed banks ranged from twenty-three to thirty in 1977, twelve to fourteen in 1978 and twelve to seventeen in 1979, with generally fewer species occurring on ploughed plots than on uncultivated plots (Table 5). However, relatively few (three to four) were present at an appreciable density (Table 6). Although there were differences in composition of seed banks between sites, the most frequent species were *Juncus bufonius*, *Alopecurus myosuroides*, *Poa annua*, *Stellaria media*, *Polygonum aviculare*, *Tripleurospermum maritimum* ssp *inodorum*, *Anagallis arvensis* and *Viola arvensis*.

DISCUSSION

Considerable difficulties may be experienced in the determination of buried seed content both in obtaining statistically representative samples and in ensuring that total seed content has been accurately determined (Kropáč 1966; Major & Pyott 1966; Jensen 1969; Harper 1977; Roberts 1981). Two methods are widely adopted for estimating seed numbers in soil samples and involve either physical separation of seeds or germination and assessment of seedling emergence. Estimates of the total viable and non-viable seed content of the seed sample requires soil washing and flotation, but such techniques are both laborious and time consuming. Malone (1967) and others have improved these procedures but only for determining viable seeds. More recently Fay & Olsen (1978) and Standifer (1980) have developed techniques for determining total seed content in soil.

Alternatively, soil samples may be placed in earthenware pans and the seeds germinated. This does not take account of the seeds which die within the germination period, or of seeds having a protracted dormancy, e.g. members of the Leguminosae. Nonetheless, this procedure has been widely adopted in long-term studies of arable and grassland seed banks (Brenchley & Warington 1930; Champness & Morris 1948; Budd, Chepil & Doughty 1954). Problems of obtaining statistically valid numbers of representative samples have been considered by Champness (1949), Rabotnov (1956) and Roberts (1958). Roberts concluded that a large number of small samples is preferable to a small number of large ones, by reducing the likelihood of problems of seed aggregation as shown by Champness (1949).

Number and distribution of seeds

Harper (1977) states that 'in most habitats occupied by higher plants the numbers of individuals present as dormant propagules vastly exceed the numbers present as growing plants'. In the present study, excluding Compton, the average buried seed population for 1977 was approximately 4200 m⁻². The results of the present investigation confirm earlier studies in that most seedlings emerged during the first year after sampling, but some species with protracted dormancy emerged over a period in excess of 2 years (Brenchley & Warington 1930, 1936; Budd et al. 1954; Hyde & Suckling 1953). In contrast to several other studies, distribution of seeds was variable between depths. Kropáč (1966) and Roberts (1970) generally found that in a crop rotation with thorough cultivation (particularly ploughing) seeds became fairly uniformly distributed throughout the working depth. However, the present results may be influenced by the absence of seed return. Roberts (1958, 1962) has demonstrated that appreciable seed losses by germination occur during the first 2 years following the prevention of seed return. For example, an average population of 229×10^6 seeds per acre declined by 62% in the first year following the prevention of seed return and by 81% of the original level after 2 years (Roberts 1958). Usually, seed losses by germination tend to be mainly restricted to the uppermost horizons of the soil profile (Bibbey 1935; and Chepil 1946b). The disproportionate loss at these levels will be offset by seed return and hence distribution will remain relatively uniform. The converse will occur when seed return is prevented as is apparent from the present study. Similarly, Jan et al. (1976), Jan & Faivre-Dupaigre (1977) and Fourbet et al. (1977) report that numbers of viable seeds decrease rapidly on the surface of uncultivated soil when herbicides are effective. However, if seed return on uncultivated plots is not prevented, then a situation comparable to that of grassland could develop with greater numbers of seeds in the surface horizons (Brenchley 1918; Chippindale & Milton 1934).

This is evident in the samples collected from Compton Beauchamp in 1979 following the failure to control grassweeds in 1978. Kropáč (1966) also reported the accumulation of weed seeds in the stubble layer of lucerne when weed control was inadequate.

Although there was no apparent relationship between species association and depth, a few species, e.g. *Stellaria media*, became rapidly depleted through germination from the surface horizon of uncultivated plots, whereas species with more protracted dormancy, e.g. *Papaver rhoeas* persisted.

Seed decline

Greater numbers of seedlings were obtained in samples taken from uncultivated plots, suggesting that seed decline (through germination) is more rapid in cultivated soil. The greater density of seedlings on ploughed plots reported previously (Froud-Williams et al. 1983) provides further evidence for this and confirms earlier observations (Roberts & Dawkins 1967; Roberts & Feast 1973a, b). Roberts & Dawkins (1967) estimated a decline of 22% per year in the absence of cultivation compared with 30% with two cultivations and 36% with four cultivations. In the present study a decline of 52.4% was recorded on uncultivated plots as compared with 72.4% for ploughed plots at Compton Beauchamp during the period 1977-1978. Similarly losses at Englefield were 50.2% and 62.6% respectively. Differences in rate of seed decline between treatments at Northfield were less marked, although in 1977 greater numbers of seed were present in samples taken from uncultivated plots. It is apparent that losses of seed by successful germination alone could not account for these substantial losses. Schafer & Chilcote (1970) have implicated post-germination mortality as a possible reason for this discrepancy. Barralis (1972) observed that in a crop rotation, emergence of seedlings in April represented on average only 5.6% of the viable seeds present in the top 10 cm of soil. Only a small percentage of the buried seed reserves contribute to the recruitment of seedlings. For example, assessments at Englefield in spring 1977 indicated that seedlings amounted to only 0.3% of the buried seed bank on uncultivated plots and 1.9% on ploughed plots. For plots cultivated twice a year, Roberts & Feast (1973a) report that only 6% of the viable seeds emerge as seedlings and Roberts & Ricketts (1979) estimated that between 3 and 6% of the viable seed emerged as seedlings in a year with adequate moisture and even less when there were dry seasons following cultivation. Although values reported here are substantially lower than those reported by Roberts and co-workers, they refer to one seedling assessment only.

The rate of seed decline was relatively uniform between depths on uncultivated plots with the exception of Compton Beauchamp, although, initially, the lower density of seed in the surface horizon suggests that seed decline had previously been more rapid, in agreement with Brenchley & Warington (1936), Chepil (1946a) and Roberts & Feast (1972). In contrast, the rate of seed decline on ploughed plots was not uniform with depth but fluctuated annually. This is consistent with annual soil inversion adjusting the relative depths of seed reserves.

Relationship between actual and potential flora

The discrepancy between species composition of the seedling flora and the seed bank of uncultivated plots is best illustrated by *P. aviculare*. For, although poorly represented in the seedling flora, *P. aviculare* was a major constituent of the seed bank. Similar results have been reported by Kropáč (1966) and Jensen (1969). The dissimilarity between actual

and potential flora of grassland has been stressed by Chippindale & Milton (1934), Dore & Raymond (1942) and Champness & Morris (1948).

In arable situations, vegetatively-reproducing species are frequently evident within the actual weed flora but contribution to the weed seed bank is relatively poor (Kropáč 1966; Jensen 1969). The dominance of annual species found here is generally typical of arable soils, but in contrast to the results of Jensen, perennial species were less evident in the vegetation phase than in the seed bank. For example, at Englefield and Northfield in 1977 perennial species contributed only 0.3% and 2.2% of the actual weed flora respectively, but comparable values for the potential weed flora were 24% and 9.4%. At Englefield, Agrostis gigantea made a large contribution to the seed bank. However, at Compton Beauchamp perennial species accounted for 29% of the actual and 9% of the potential weed flora which is more comparable with the findings of Jensen (1969). Furthermore, Agropyron repens was dominant in the stubble of uncultivated plots in 1978 but was not present in the seed bank. The very large contribution of J. bufonius to the buried seed bank and its apparent absence from the vegetation has been reported elsewhere (Jensen 1969). This is perhaps not surprising as seed production by Juncus spp may be considerable, up to 700 000 per plant (Salisbury 1961) and the seeds have a long life-span.

The weed flora at each site was dominated by relatively few species, the majority of species fulfilling only a minor role. Most frequently recorded species in these studies include *P. aviculare*, *T. maritimum* and, following a history of grassland, *P. annua*. In a survey of buried weed seed populations in South Warwickshire and North Oxfordshire, *P. annua*, *S. media* and *P. aviculare* were amongst the most frequent species (Roberts & Neilson 1979).

Although crop rotation was employed at three sites there was no evidence of changing dominance between years. Brenchley & Warington (1930) report markedly different proportions of species in different crops but the main differences they found were between autumn and spring sowing, whereas in the present study all crops were autumn sown.

CONCLUSION

In the absence of further seed-return, buried seed populations will decline more rapidly with cultivation than no cultivation, but seedling populations will initially be greater with cultivation. However, as weed seed return is not likely to be entirely prevented in commercial practice, freshly shed seed will continue to present a problem particularly in reduced cultivation systems. Furthermore, any departure from reduced-cultivation will result in exhumation of buried seed, reducing any beneficial effect of weed control previously obtained. Nonetheless, periodic return to ploughing may be essential if suitable herbicides are not available for the control of specific weeds.

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REFERENCES

Bachthaler, G. (1974). The development of the weed flora after several years direct drilling in cereal rotations on different soils. *Proceedings British Weed Control Conference*, pp. 1063–1071.

- Barralis, G. (1972). Evolution comparative de la flore adventice avec ou sans desherbage chimique. Weed Research, 12, 115–127.
- **Beuret, E. (1980).** Influence de la monoculture et des methodes de travail du sol sur la flore adventice et le stock granier du sol. Comptes Rendus du 6^{eme} Colloque International sur l'Ecologie la Biologie et la systematique des mauvaises herbes, Montpellier, pp. 389-399.
- Bibbey, (1935). The influence of environment upon the germination of weed seeds. Scientific Agriculture, 16, 141-150.
- Brenchley. W. E. (1918). Buried weed seeds. Journal of Agricultural Science, Cambridge, 9, 1-31.
- Brenchley, W. E. & Warington, K. (1930). The weed seed population of arable soil. I. Numerical estimation of viable seeds and observations on their natural dormancy. *Journal of Ecology*, 18, 235–272.
- Brenchley, W. E. & Warington, K. (1936). The weed seed population of arable soil. III. The re-establishment of weed species after reduction by fallowing. *Journal of Ecology*, 24, 479–501.
- Budd, A. C., Chepil, W. S. & Doughty, J. L. (1954). Germination of weed seeds. III. The influence of crops and fallow on the weed seed population of the soil. Canadian Journal of Agricultural Science, 34, 18–27.
- Champness, S. S. (1949). Note on the technique of sampling soil to determine the content of buried viable seeds. *Journal of the British Grassland Society*, 4, 115–118.
- Champness, S. S. & Morris, K. (1948). The population of buried viable seeds in relation to contrasting pasture and soil types. *Journal of Ecology*, 36, 149–173.
- Chepil, W. S. (1946a). Germination of weed seeds. I. Longevity, periodicity of germination and vitality of seeds in cultivated soil. *Scientific Agriculture*, 26, 307–346.
- Chepil, W. S. (1946b). Germination of weed seeds. II. The influence of tillage treatments on germination. *Scientific Agriculture*, 26, 347–357.
- Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1962). Flora of the British Isles. Cambridge University Press, Cambridge.
- Chippindale, H. G. & Milton, W. E. J. (1934). On the viable seeds present in the soil beneath pastures. Journal of Ecology, 22, 508-531.
- Cook, R. (1980). The biology of seeds in the soil. *Demography and Evolution in Plant Populations* (Ed. by O. T. Solbrig), pp. 107–129. Blackwell Scientific Publications, Oxford.
- Cussans, G. W., Moss, S. R., Pollard, F. & Wilson, B. J. (1979). Studies of the effects of tillage on annual weed populations. The Influence of Different Factors on the Development and Control of Weeds, pp. 115–122. Proceedings of the European Weed Research Society Symposium. Mainz.
- Dore, W. G. & Raymond, L. C. (1942). Pasture Studies XXIV. Viable seeds in pasture soil and manure. Scientific Agriculture, 23, 69-79.
- Fay, P. K. & Olson, W. A. (1978). Technique for separating weed seed from soil. Weed Science, 26, 530-533.
- Fourbet, J. F., Huet, Ph. & Jan, P. (1979). Problemes poses par la simplification des systemes de culture dans la lutte contre les mauvaises herbes. The Influence of Different Factors on the Development and Control of Weeds, pp. 123–133. Proceedings of the European Weed Research Society Symposium, Mainz.
- Froud-Williams, R. J., Drennan, D. S. H. & Chancellor, R. J. (1983). Influence of cultivation regime on weed floras of arable cropping systems. *Journal of Applied Ecology*, 20, 187–197.
- Harper, J. L. (1977). Population Biology of Plants. Academic Press, London.
- Hyde, O. C. & Suckling, F. E. T. (1953). Dormant seeds of clovers and other legumes in agricultural soils. New Zealand Journal of Science and Technology, 34, 375–385.
- Jan, P., Fontaine, A. & Dumont, R. (1976). Incidence de la simplification du travail de sol sur le flore adventice. Simplification de Travail du Sol en Production Céréalière, pp. 205-218. I.T.C.F. Paris.
- Jan, P. & Faivre-Dupaigre, R. (1977). Incidence des facons culturales sur la flore adventice. Different Methods of Weed Control and their Integration, pp. 57-64. Proceedings of the European Weed Research Society Symposium, Uppsala.
- Jensen, H. A. (1969). Content of buried seeds in arable soil in Denmark and its relation to the weed population, Dansk Botanisk Arkiv, 27, 1-56.
- Kropáč, Z. (1966). Estimation of weed seeds in arable soil. *Pedobiologia*, 6, 105–128.
- Lockett, P. M. & Roberts, H. A. (1977). Weed seed populations. Report of the National Vegetable Research Station for 1976, 111.
- Major, J. & Pyott, W. T. (1966). Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio, 13, 253–282.
- Malone, C. R. (1967). A rapid method for enumeration of viable seeds in soil. Weeds, 15, 381–382.
- Pollard, F. & Cussans, G. W. (1976). The influence of tillage on the weed flora of four sites sown to successive crops of spring barley. *Proceedings of the British Crop Protection Conference—Weeds*, 1019–1028.
- Pollard, F. & Cussans, G. W. (1981). The influence of tillage on the weed flora in a succession of winter cereal crops on a sandy loam soil. *Weed Research*, 21, 185–190.
- **Rabotnov, T. A. (1956).** Some data on the content of living seeds in soils by meadow communities. *Akademika V.N. Sukacheva K 75-letiyo so diua rozhdeniia*. Akad. Bauk SSSR, Moskva-Leningrad, pp. 481–499.
- Roberts, H. A. (1958). Studies on the weeds of vegetable crops. I. Initial effects of cropping on the weed seeds in the soil. *Journal of Ecology*, 46, 759–768.
- **Roberts, H. A. (1962).** Studies on the weeds of vegetable crops. II. Effect of different primary cultivations on the weed seeds in the soil. *Journal of Ecology*, **50**, 803–813.

- Roberts, H. A. (1963a). Studies on the weeds of vegetable crops. III. Effect of different primary cultivations on the weed seeds in the soil. *Journal of Ecology*, 51, 83-95.
- Roberts, H. A. (1963b). Studies on the weeds of vegetable crops. IV. Further observations on the effects of different primary cultivations. *Journal of Ecology*, 51, 323-332.
- Roberts, H. A. (1970). Viable weeds seeds in cultivated soils. Report of the National Vegetable Research Station for 1969, pp. 25-38.
- Roberts, H. A. (1981). Seed banks in soils. Advances in Applied Biology, 6, 1-55.
- Roberts, H. A. & Dawkins, P. A. (1967). Effect of cultivation on the numbers of viable weed seeds in soil. Weed Research, 7, 290-301.
- Roberts, H. A. & Feast, P. M. (1972). Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research*, 12, 316–324.
- Roberts, H. A. & Feast, P. M. (1973a). Changes in the numbers of viable weed seeds in soil under different regimes. Weed Research, 13, 298–303.
- Roberts, H. A. & Feast, P. M. (1973b). Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *Journal of Applied Ecology*, 10, 133–143.
- Roberts, H. A. & Neilson, J. E. (1980). Weed seed populations. Report National Vegetable Research Station for 1979, pp. 127-128.
- Roberts, H. A. & Stokes, F. G. (1965). Studies on the weeds of vegetable crops. V. Final observations on an experiment with different primary cultivations. *Journal of Applied Ecology*, 2, 307–315.
- Roberts, H. A. & Ricketts, M. E. (1979). Quantitative relationships between the weed flora after cultivation and the seed population in the soil. *Weed Research*, 19, 269–275.
- Russell, E. W. & Mehta, N. P. (1938). Studies in soil cultivation. VIII. The influence of the seed bed on crop growth. *Journal of Agricultural Science*, 28, 272–298.
- Salisbury, E. J. (1961). Weeds and Aliens. Collins, London.
- Schafer, D. E. & Chilcote, D. O. (1970). Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. *Crop Science*, 10, 342-345.
- Soriano, A., Zeiger, E., Servy, E. & Suero, A. (1968). The effect of cultivation on the vertical distribution of seeds in the soil. *Journal of Applied Ecology*, 5, 253-257.
- Standifer, L. C. (1980). A technique for estimating weed seed populations in cultivated soil. *Weed Science*, 28, 134–138.

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