

CHAPTER 7

Population Studies

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Any approach to wild oat control must ultimately be concerned with wild oat populations and, in particular, the regulation of those populations according to the needs of the individual grower (see Chapter 6, Control Objectives and Systems, p. 114). Some understanding of wild oat population dynamics is therefore essential.

Wild oats are such serious and persistent weeds that there has long been an interest in their population dynamics and the influence of environmental factors. The work involved is frequently laborious and long-term in nature and, although both practical and academic workers have studied the problem, the literature is limited.

One problem common to all studies of population is that of deciding the parameter(s) by which population can best be measured. Thus, many field studies have been based on assessments of wild oat panicle density at cereal harvest. These have the advantages of simplicity: if all the variable factors acting on a succession of cereal crops could be eliminated, panicle density would be an admirable way of monitoring long-term population changes. Indeed it may well be that, over a very long term, variations in time of planting, climate, cereal disease incidence, etc, do cancel out so that simple assessment methods are valid.

However, assessments of panicle density give only a poor indication of spring emergence of seedlings; seedlings may be killed or die naturally or may flourish to produce more than one panicle per plant. Conversely panicle density gives only a poor indication of the future potential of the weed population unless seed numbers per panicle are also recorded; panicle size may range from 1 to 500 seeds per panicle.

In this chapter the literature has been reviewed against the background of a simple population cycle (Fig. 7.1) in which the seed is taken to be the basic unit of population. This has several disadvantages and one important advantage. The plasticity of wild oat growth in crops can be accommodated by considering numbers of seeds as a simple integration of seedling survival, number of fertile tillers and size of panicles. It can be postulated that seed number also provides an integration of competitive ability of a wild oat population. This is more doubtful scientifically and is discussed elsewhere. In any case it is suggested that, as far as possible, seedling populations are best expressed in terms of their potential ability to produce seed. This schematic cycle differs from the more elaborate scheme devised by Sarukhan (1974) to

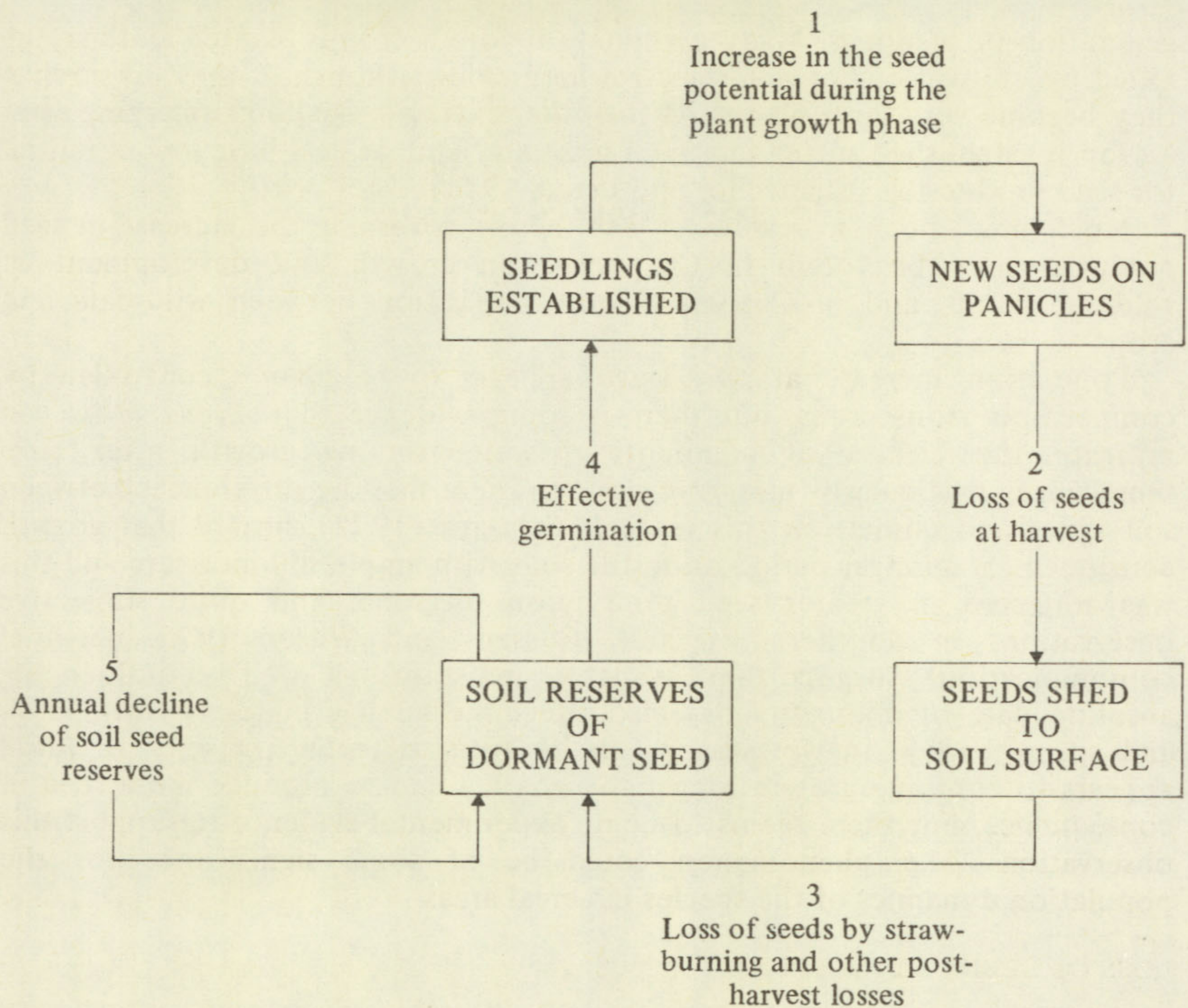


Fig. 7.1. A schematic population cycle for wild oats, with the seed as the basic unit of population.

describe the reproductive balance of *Ranunculus* species, partly because wild oats have no vegetative propagules. Furthermore it is convenient to divide the cycle into a series of discrete pathways during which the population can be said to be largely under the influence of different sets of environmental factors.

INCREASE IN SEED POTENTIAL DURING THE PLANT GROWTH PHASE

The reproductive capacity of the weedy *Avena* species is potentially enormous and, in practice, immensely variable. Thus, *Avena fatua*, grown free from competition in the English lowlands, can produce many fertile tillers giving a potential of around 2000 seeds/plant. The reproductive capacity of the same species in the natural annual grasslands of California was recorded as between 6 and 20 seeds/surviving plant by Marshall and Jain (1967). In cereal crops the number of seeds per surviving plant ranges widely about a mode of 40-50.

This figure is scarcely true for the reproductive capacity of a whole

generation of seedlings. Many germinate before a crop is planted and may be killed by cultivations or non-selective herbicides although, if they do survive, they become very large plants. At the other extreme, seedlings emerging after a crop is established suffer very high mortality and, at best have low potential for seed production (Chancellor and Peters 1974).

Much more detailed reviews of the factors governing the increase in seed potential may be found in Chapter 4 on growth and development of wild-oat plants and in Chapter 5 on competition between wild-oats and crops.

Population increase at this stage appears to be mainly controlled by competition from crops, but there is some evidence that *Avena fatua* can mitigate the effects of competition by continuing growth after crop senescence, particularly in spring barley. There may be differences between soil types and climate in this respect. Odgaard (1972) showed that growth continued for a longer period on fertile soils with ample soil moisture and this was reflected in greater seed production. Personal and quite subjective observations in Southern England (Cussans and Wilson 1975, personal communication) suggest that available moisture, as well as influencing absolute date of maturity, may also affect the relative maturity of *A. fatua* and spring barley. In wet seasons, or on moisture retentive soils, *A. fatua* appears to continue growth longer than barley and to produce more seed in consequence, but there seems to be no experimental evidence to support this observation. The phenomenon could be of some significance for the population dynamics of the species in cereal areas.

LOSS OF SEEDS AT HARVEST

Some very early harvested crops, eg peas or arable silage, may remove very large numbers of seeds. This is discussed more fully in Chapter 7 on cultural control. In most crops, however, ripening and natural shedding of wild-oats is well advanced at harvest (Wilson 1970a). The degree of shedding which has occurred by harvest is influenced by weather and other factors. In cereal crops in Southern England it commonly appears to exceed 90%, so that less than 10% of the seed is available for redistribution at harvest. Records by Wilson (1971a, and unpublished) show that, at harvest, only about 20% of the wild oat seeds available for redistribution are removed with the combine harvested grain, whilst the proportion removed with baled straw may be even smaller, of the order of 0.5 to 2%.

It appears therefore that loss of seed from a population at harvest, although very much influenced by time of crop maturity, is generally small, commonly less than 2% of the total seed produced. This small proportion may have a major effect in dissemination of these weeds over wider geographical areas (see p. 57-60) but is a minor factor in the dynamics of established populations.

POST-HARVEST LOSSES

The freshly shed seed of wild oats is equipped with a self-burial mechanism whereby the awn twists with alternate wetting and drying and this drives the

seed horizontally across the soil surface. The seed may then be driven below a stone or into a soil crack or buried in loose surface mould. The process is relatively inefficient. Marshall and Jain (1967) found in California that the mean lateral movement was 5-8 cm. In these studies *A. barbata* penetrated more deeply into the soil than *A. fatua* but neither achieved very deep burial.

Such burial protects the seed from predation by birds and mice, but not always successfully. Marshall and Jain (1970) recorded losses due to predation ranging from 1-65% of the total seed load. Burial may also give protection from the effects of burning straw, whilst Wilson (1972) showed that seeds protected from all these hazards could still suffer a natural loss of viability when exposed on the soil surface, but not when buried.

Burial by cultivation is much more effective than self burial in protecting the recently shed seed. Thus time of cultivation in the autumn may be an important factor in controlling the loss of seed from a population. Wilson and Cussans (1972, 1975) showed that early cultivation could more than double the rate of population increase and Whybrew (1964) reported similar but less marked responses to cultivation. These factors are reviewed more fully in Chapters 8 (Cultural Control) and 10 (Plant Health and the Possibilities for Biological Control). Clearly these early losses of seed can play an important role in population changes and since some of the factors are influenced by cultural activities they are important in determining survival in cropped land.

EFFECTIVE GERMINATION OF SEEDS FROM SOIL RESERVES

This aspect of the cycle is discussed in Chapter 4 on Growth and Development of Wild Oat Plants.

It is difficult to quantify the relationship between seed reserves and effective germination, conditioned as it is by both natural factors and human activity. Seed must first be released from dormancy; this can be a natural process or it can be induced by straw-burning (Thurston 1958, Wilson and Cussans 1975) or by cultivation. When the seed has lost dormancy, conditions must be suitable for germination although Holroyd (1964a) and Fykse (1970b) have both showed that *A. fatua* seedlings may start to grow from depths too great for successful emergence. Fykse showed that emergence was most successful from a depth of 5 cm in bare soil, he recorded no seedling emergence on grass swards.

It appears from this work by Fykse and others that some cultivation may be a pre-requisite for successful seedling establishment in northwest Europe. This cannot be universally true, however, since *A. fatua* is a natural constituent of grassland in California and parts of Australia. Plants are also found on motorway embankments and field margins in the United Kingdom, notably when seed is freshly introduced, but populations do not seem to persist in dense grass swards. In arable land it has been very widely accepted that more frequent cultivations in spring lead to greater stimulation of germination, but this is by no means established. There is little clear evidence that cultivation beyond a basic minimum does increase germination (Thurston 1961). In the dynamics of a population in cropped land, there must be in any case a clear distinction between total and effective

germination. Effective germination results in established seedlings with a high potential for seed production and such seedlings must emerge in the early stages of crop growth (Chancellor and Peters 1972).

Effective germination can therefore be affected by cultural factors, notably cultivation and time of crop establishment, and by natural factors such as climate and the age structure of the population. Wilson and Cussans (1975) showed, for one population in Oxfordshire, that the fraction of the seed reserves less than one year old was less than half as successful at producing seedlings as the older reserves. In this experiment the more recent seed was more numerous so despite its lower success rate this fraction contributed up to 90% of the total seedling numbers. Clearly, though, if the ratio of recent to older seed varies, the ratio of seedlings to total seed reserves would also be expected to vary. In the populations studied by Wilson and Cussans (1975) the proportion of the viable seed reserves, recorded in February, which gave rise to seedlings later in the spring ranged from 12 to 38%, depending on the age of the seed and the cultural treatment it received. These figures refer to total seedling emergence; the numbers of effective seedlings were lower.

In this study, and in earlier work by Thurston (1961a), the periodicity of seedling emergence was uninfluenced by depth or time of cultivation, by seed age or by straw burning the previous autumn. Other experiments (Wilson and Cussans 1972) indicated slower emergence where plots were not cultivated at all but a similar seedling emergence pattern on all cultivated plots.

These findings suggest that the main factors controlling the ratio of total seedlings to effective seedlings are climate, time of planting the crop, and attendant cultivations.

ANNUAL DECLINE OF SOIL SEED RESERVES

The study by Wilson and Cussans (1975) indicated two major periods of loss of seeds from an established population of *A. fatua*. The first loss of newly shed seeds from the stubble surface—has already been discussed. The second major period of seed loss occurred between February and June, when 40-48% of the viable seeds disappeared without producing seedlings. These losses appear to be attributable to unsuccessful germination (see Kropáč 1966). After seedling emergence was complete, seed populations remained fairly static, with little loss between June and the following February. The autumn germination of *A. fatua* was due mainly to recently shed seed and had little effect on the buried seed reserves.

Longevity of seed may vary with soil type and climate. Fykse (1970b) transported soils to soil pits so as to study the effects of soil type, climate, land use and their interactions. Seeds of *A. fatua* persisted longer on clay soil and on grass plots. Regardless of other factors, survival was much greater at the coastal site than in the cooler, drier climate inland. This climatic difference did, however, seem most marked in the first year of the 3½-year experiment.

Detailed knowledge of the rate of loss of seeds is still sadly deficient but some detailed studies have been made. In addition some studies of continued

germination in the absence of shedding give useful guides to the decay of seed populations although it is dangerous to assume that seedling numbers always reflect accurately the residual seed populations. This work suggests two broad areas of agreement.

A number of attempts to record survival of *A. fatua* in grassland have been reviewed more fully in Chapter 8, Cultural Control. These indicate a rate of loss of the order of 50% per annum in sown temperate grassland.

In cultivated arable land, the annual loss of seeds appears to be much more rapid, in some cases the annual loss being of the order of 80% (Gummeson 1972b, Wilson and Cussans 1975). This is by no means clear. Fykse (1970b) reported a seed decline on bare soil which, although more rapid than that on grass plots was of the same order. This could perhaps be explained by the fact that Fykse planted seeds at 5 or 20 cm and subsequently kept the soil bare but did not cultivate deeply as in normal arable practice. This supports the results of Thurston (1961) who found the longest persistence of *A. fatua* on plots where the seeds were ploughed in and subsequent cultivations were shallow. However, Thurston recorded rates of reduction of seedling emergence rather lower than those recorded by Gummeson (1972b) and Wilson and Cussans (1975) on natural populations of *A. fatua*. *A. fatua* proved to be more persistent than *A. ludoviciana* in this experiment.

STUDIES OF THE WHOLE POPULATION CYCLE

Selman (1970c) reported that, at Boxworth Experimental Husbandry Farm, an uncontrolled population of *A. fatua* on plots continuously cropped with spring barley from 1959 to 1964, increased annually by a factor of approximately 2.7 (range 1.3 to nearly 6). Selman also discussed some of the potential practical applications of such knowledge. It was suggested that, in some circumstances, a herbicide regime which maintained a weed population at a low level might be an economic choice. Such a herbicide regime would have to match in efficiency the potential for population increase of the cultural and cropping system. In theory at least, a farming system which allowed the weed population to double annually, could be maintained at a constant level by a herbicide programme which ensured 50% reduction in weed seed return. Selman pointed out that such a balance could be achieved in some cases by intermittent use of herbicides.

Wilson and Cussans (1975) studied population changes on plots subjected to a range of cultivation treatments with or without straw burning. Where seed was allowed to shed the average increase factor was 3.4 on plots where straw was removed, and 2.5 on burnt plots, increases of the same order as those recorded by Selman. In each case, however, early stubble cultivation greatly increased the rate of population increase so that the overall range for the increase factors was from 1.6 to 4.4.

It can be noted that all of these values for year to year population increase fall into the range which would be expected if the numerical values in Table 7.1 were assigned to the five pathways. These imperfect correlations cannot in any way be said to represent predictions but it would appear that this gives a simple summary of the population dynamics cycle of *A. fatua* as it has so

Table 7.1 *The wild oat population cycle in spring barley: a range of observed values for multiplication factors in each of the five pathways*

Pathway or phase	Multiplication factor
1. Increase in seed potential during plant growth phase	40-50
2. Loss of seeds at harvest	0.90-0.98
3. Loss of seeds by straw-burning or other post-harvest losses	0.25-1.00
4. Effective germination	0.09-0.12
5. Annual decline of soil seed reserves	0.20-0.25

far been recorded in continuous spring barley cultivation in Southern England.

These studies of the population dynamics of *Avena fatua* are very limited in scope, being restricted to temperate spring cropping for example. There is ignorance particularly of the numerical relationships between seeds in the soil and successfully established seedlings, although some at least of the theory is reasonably well understood.

Population dynamics studies are laborious and time consuming so that practical benefits do not flow easily from the original concept. However, such knowledge is of great practical value. Indeed, such research is a meeting ground for practitioner and theoretician. In view of the world-wide importance of these weeds in land intensively cropped with cereals it is to be hoped that such research will continue and ultimately simple population models could be prepared for at least some of the diverse situations in which these species are weeds.