Comparative ecology of four brome grasses.

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by

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Abstract

Changes in husbandry practices frequently alter the composition and abundance of plant species that comprise the weed flora of arable ecosystems. This thesis examines differences in the ecology of four brome grasses that may account for the present variation in their relative abundance. The species investigated were *Bromus commutatus* Schad., *B. interruptus* (Hack.) Druce, *B. mollis* L. and *B. sterilis* L.

Studies of selected aspects of the autecology of these species detected differences in their germination biology. In laboratory experiments, all four species showed high germination over a range of temperatures (12-25 °C). *B. interruptus* displayed rapid germination at low water availabilities that delayed the rate of germination of the other species. This difference was also observed on a stubble surface in the field. Seedling establishment from depth (>100 mm) was limited in all species though differences did exist in the proportion establishing from shallow depths (50 mm). Species also exhibited differing rates of seed dissemination and in *B. commutatus* and *B. mollis* this varied for plants grown in monoculture and in a cereal crop. In the presence of a crop, *B. interruptus* showed the slowest rate of dissemination.

Investigation of the growth of populations of the grasses in conditions simulating those of a field margin indicated that all four species exhibited the potential to persist in such habitats. Plastic fecundity, in response to increased brome density, was recorded for all four species as was reduction in yields due to competition with a crop. Statistical fits of the yield/plant data to a model describing the yield/density relationship highlighted the different responses of the four species to treatments of increasing crop density and a wheeling treatment early in the life cycle of the crop. The competitive interaction of *B. interruptus* and *B. sterilis* was investigated in a pot experiment involving species in mixture over a wide range of densities. Results indicated that *B. sterilis* was a stronger competitor than *B. interruptus*, when both species germinated simultaneously.

Observations on seed dispersal, both natural seed shadows and the distribution of seeds as influenced by the husbandry practices of seed bed preparation and combine harvesting are reported. For all four species, seed dispersal by natural means was limited within a range upto 1.5 m. Differences were apparent amongst the species, *B. interruptus* showing the most restricted dispersal whereas *B. mollis* exhibited the maximum. Under soil tillage, the shape of the distribution pattern of the seeds was determined by the cultivation implement used and to a lesser extent seed size, in general smaller seeds moving the furthest. The maximum distances moved by seed on the soil surface during seed bed preparation were approximately twice that observed in naturally dispersing seeds. Combine harvesting had a marked effect on seed dispersal patterns, greatly increasing the distances moved by seeds. Differences in the proportions of seed returned to the stubble and entering the grain tank were detected which related to seed size, higher proportions of the smaller seed being deposited with the chaff. These studies showed that combine harvesting of an arable crop will have a significant impact on the dissemination of seed of weed species that naturally tend to retain seed in the infructescence. Of the four bromes the spread of *B. interruptus* is likely to be enhanced the most by this means

A range of differences were detected amongst the species which, at least partly, explain the relative abundances recorded in the U.K. Implications of these results in relation to the possible reintroduction of *B. interruptus*, using arable headlands as a conservation habitat are discussed.

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Plate 1 A panicle of *Bromus interruptus* (X5)

Chapter 1

Introduction

1. Introduction

A plant can be considered as a weed "if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated plants)" (Baker, 1965). The characteristics of weeds have been the subject of numerous investigations usually in relation to their detrimental effects on crop production (Cousens, 1985; Firbank & Watkinson, 1985), attempted elimination or control (Attwood, 1980), or as examples of evolution in progress (Harper, 1956; Georghiou, 1972; Grignac, 1978). Due to the rapid decline in both the number and abundance of some weed species, brought about by changing agricultural practices (section 1.2), several weed species have become the subjects for study in the interests of conservation (Perring, 1970; Ratcliffe, 1977). Hodgson (1986) stated that "comparative studies of common and rare species appear to provide a promising approach towards an understanding of the reasons for both commonness and rarity". His assertion has already been proven by several studies of the North American flora (Primack, 1980; Fielder, 1987), particularly the extensive work on sparse and common tallgrass prairie species (Rabinowitz, 1978; Rabinowitz *et al.*, 1979; Rabinowitz & Rapp, 1981; Landa & Rabinowitz, 1983). Such comparative investigations can provide information on specific features of the biology of a species, for example idiosyncratic flower biology or seed dispersal, that may distinguish a rare species from common related species (Fielder, 1987). This thesis details a comparative study of four *Bromus* grasses, of widely varying abundance in the United Kingdom today, in an investigation of the reasons for these differences.

1.1 Species

The work reported in this thesis focuses on four brome grasses namely *Bromus commutatus* Schad., *B. interruptus* (Hack.) Druce, *B. mollis* L. and *B. sterilis* L. These four species were chosen as they display a wide range of abundance in Britain, as shown by the following distribution maps, Figure 1.1.1 (Perring & Walters, 1976) yet are closely related. *B. interruptus* is now classified as extinct (Lucas & Synge 1978) whilst *B. sterilis* is an

Figure 1.1.1 The distribution of *B. commutatus* , *B. interruptus* , *B. mollis* and *B. sterilis* in the U.K. (reproduced from Perring & Walters, 1976).

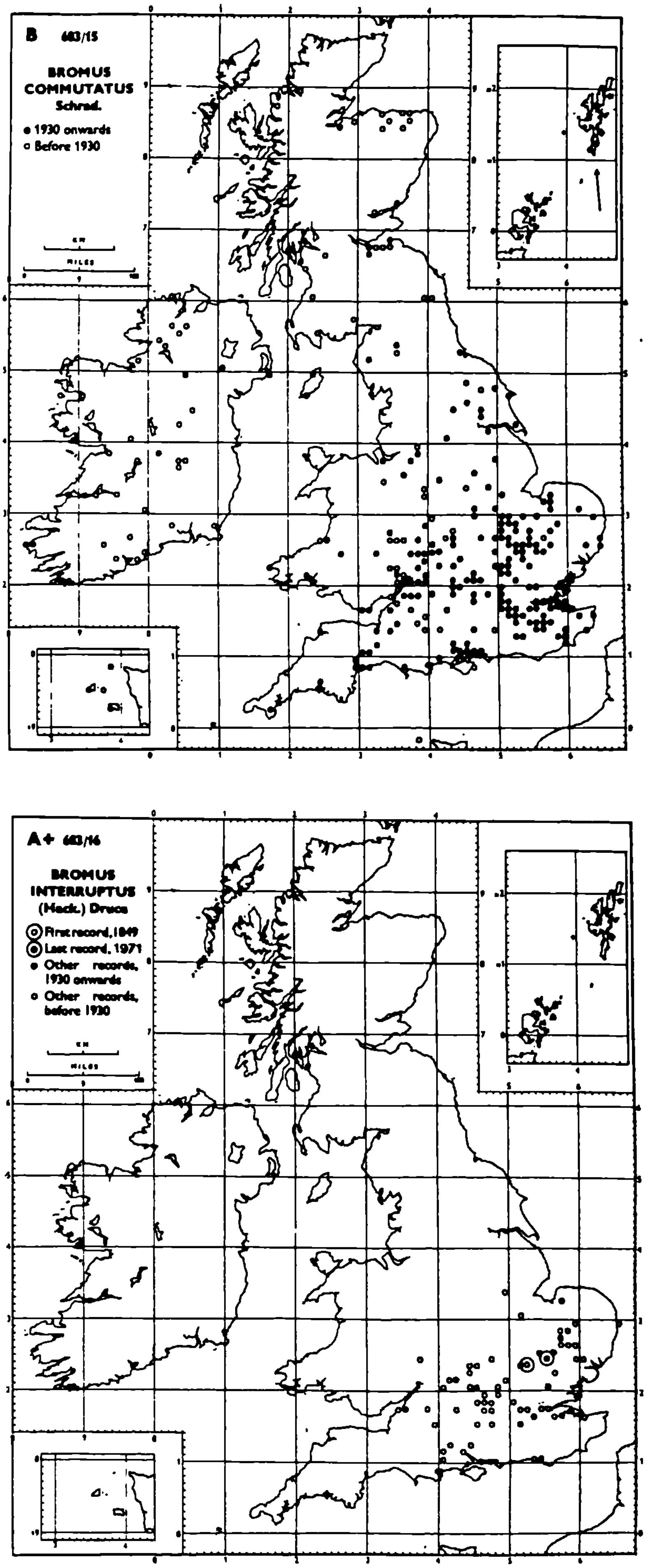
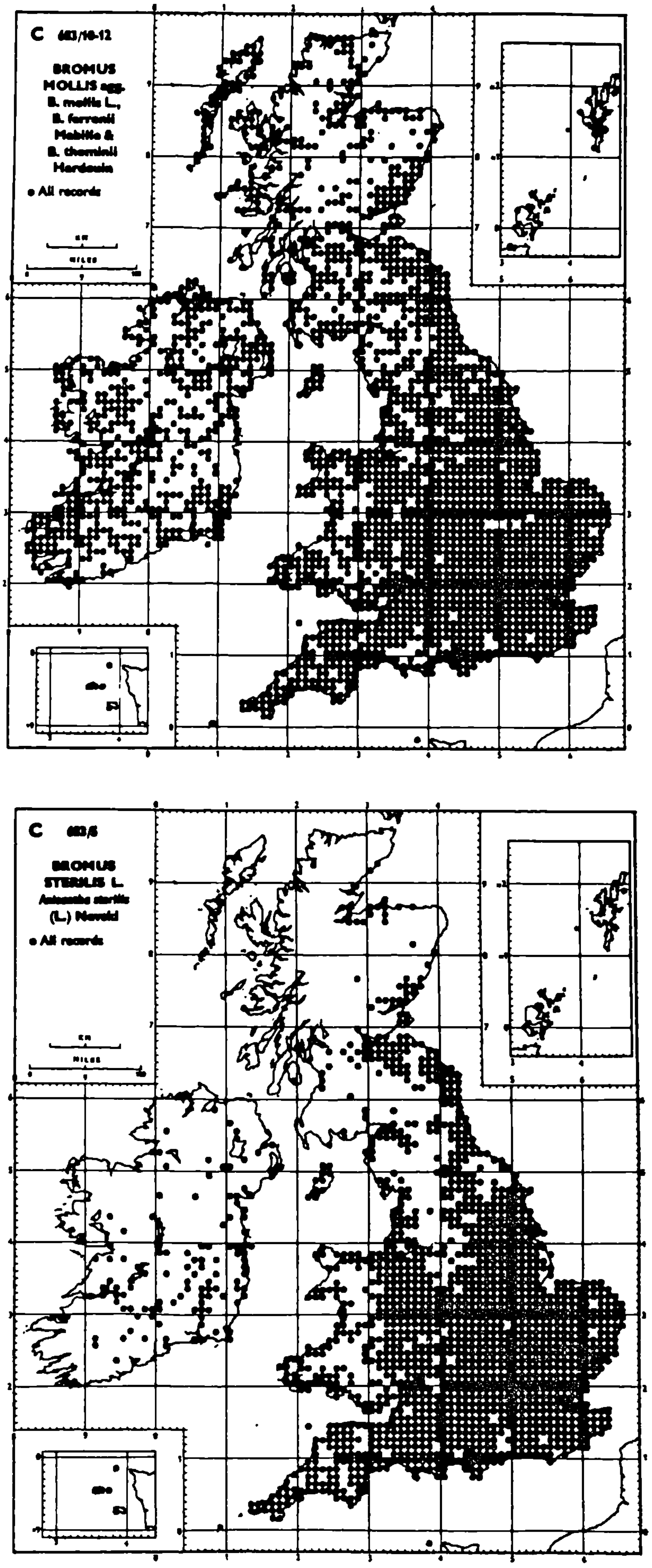


Figure 1.1.1 continued.



increasingly common arable weed. *B. commutatus* and *B. mollis* are reported to be relatively uncommon (Anon, 1989).

All four species have been shown to be distinct species on the evidence of serological data and attempted hybridisation (Smith, 1972).

B. commutatus Schad., Meadow Brome, was first recorded in 1833 and displays an annual or biennial life cycle (Hubbard, 1984). Favoured habitats include field margins, tracks and roadsides, where it can be locally abundant, as well as moist lowlands. *B. commutatus* has a scattered distribution throughout Britain though it is mostly found in the south since the 1930's where it is increasingly abundant. On a larger scale this species is found throughout Europe, North Africa and into West Asia (Hubbard, 1984).

B. interruptus (Hack.) Druce, Interrupted Brome, was first collected in 1849 when it was thought to be a subspecies of the *B. mollis* aggregate. Druce (1895) first identified *B. interruptus* as a separate species. The species shows an annual or biennial life cycle and was usually found in field margins in association with sainfoin, rye grass and clover (Hubbard, 1984). The last official recording was in 1972 (Lucas & Synge, 1978). Even for an endemic species *B. interruptus* had a limited distribution being found in only 65 10 km squares, over 27 vice counties, in southern England at the peak of its abundance in the 1920's.

B. mollis L., Soft Brome or Lop grass, was first recorded as early as 1660. This species shows considerable ecotypic differentiation in life cycle probably due to being an aggregate species (Smith, 1968). Under grazing *B. mollis* exists as a short lived perennial whilst in open habitats it displays an annual life cycle. *B. mollis* is most commonly found in meadows and on road verges and waste ground. The species is the most widespread of all the bromes being found throughout Britain, Europe and West Asia (Hubbard, 1984).

B. sterilis L., Barren Brome or Sterile Brome, was also first recorded in 1660 and like the other three species shows an annual or occasionally biennial life cycle. This species is commonly found on roadsides, hedge bottoms, field margins and waste ground preferring well drained lowland soils (Hubbard, 1984). The abundance of *B. sterilis* has increased greatly since the mid 1970's with the species now regarded as the fifth most frequent grass weed of cereals surveyed in southern England (Froud-Williams & Chancellor, 1982). The number of fields in which *B. sterilis* was found, in 1983, had increased to 15% from 9% the previous year (Chancellor & Froud-Williams, 1984). *B. sterilis* has a large distribution including the majority of Europe and spreading into South West Asia.

Table 1.1.a Comparison of the seeds of the four brome species.

Species	Seed Dimensions			
	1000	Average		Maximum
	Seed Weight	length	width	awn length
	(g)	(mm)	(mm)	(mm)
B. commutatus	7.4	8	2	10
B. interruptus	4.4	6	2.5	10
B. mollis	4.2	7	2	10
B. sterilis	9.9	12	1.5	30

All measurements taken from samples of seed stocks in October 1988

For details of seed suppliers see Appendix 1.

1.1.1 Possible origin of *B. interruptus*.

When initially identified as a separate species the possibility that *B. interruptus* was an introduction from imported seed mixtures was considered (Druce, 1897). However, no European specimens were found by Druce, at the time, to have been a possible source. The only records of *B. interruptus* in Europe, since then, have been in the Netherlands where it was considered as an introduction from Britain (Hubbard, 1984). The species is now widely considered as endemic to Britain (Smith, 1972; Hubbard, 1984; Tutin *et al.*, 1985).

Smith (1972) using serological studies, which showed the similarity of the protein spectrum of seeds of *B. interruptus* and *B. mollis* , and plant morphology suggested that

B. interruptus may be from a mutant of *B. mollis* but sufficient differences exist to justify its classification and treatment as a separate species. These differences include *B. interruptus* possessing a compact, interrupted inflorescence, very short rachilla internodes and a palea split throughout its length. With the exception of the last character these features suggest *B. interruptus* may have had an origin as a compactoid mutant of *B. mollis* (Smith, 1965). However, Smith (1965) failed to produce a similar mutation as *B. interruptus* in *B. mollis* using irradiation or mutagenic chemicals.

1.2 Agricultural history of the last fifty years

British agriculture has witnessed major changes in the last fifty years towards an increasingly productive and technological system of farming (Lloyd & Wibberley, 1977). In 1937 the government introduced a soil fertility scheme providing subsidies to farmers for liming their fields. Continued demands for food during the 1939-45 war resulted in increases in the acreage of land brought back into productive use. The 1947 and subsequent Agricultural Acts maintained incentives for farmers to continue to increase production.

One of the major postwar advancements was the introduction of the plant growth regulators 2,4 D and MCPA which replaced the old, ineffectual, pre-war herbicides. The following thirty years saw a rapid expansion in the range of herbicides available to a level of fifty herbicidal ingredients, marketed under 300 brand names, by the late 1960's (Fryer & Chancellor, 1970). With the increase in the range of herbicides available came an increase in the variety of the modes of action of the herbicides and consequently an increase in their species selectivity. Herbicidal action can occur via the disruption of numerous metabolic processes within the plant that eventually result in death, for example, inhibition of photosynthesis or respiration, failure to produce vital intermediary metabolites or the accumulation of toxic molecules (Dodge, 1990). The selectivity shown by herbicides usually depends on an interaction of several factors such as plant physiology, differential uptake and metabolism of the herbicides. Considering just one aspect, the differential uptake of herbicides, selectivity can be achieved by variation in the time of application, i.e pre or post emergence of the crop, and the position of the herbicide within the soil to exploit differences in the emergent seedling morphology or rooting depths (Caseley & Walker, 1990). For contact herbicides the leaf shape and angle are important, determining interception of sprayed liquid herbicides and the cuticle texture and weather conditions are influential as they effect retention and absorbtion of the herbicide (Dodge, 1990).

The advent of the selective herbicides has had a major influence on the weed floras associated with agriculture. In cereal fields the relative abundances of weeds has shifted dramatically (Haas & Streibig, 1982). The control of dicotyledons, within cereals, by the use of selective herbicides has lead to increases in the abundance of grass weeds. The removal of the broadleaved species has reduced the competitive pressures that formally kept the grasses in check. The increased selectivity of herbicides has resulted in the crop and weed becoming more closely related (Sagar, 1974), differences in morphology and metabolism providing opportunities for selective herbicides to differentiate amongst species.

The use of inorganic fertilizers and additions of lime, both aimed at improving soil quality and increasing production, has also influenced the weed floras. These influences are to the detriment of some species whilst of benefit to others, especially those favoured by higher nutrient soils, e.g. *Agropyron repens* L. (Haas & Streibig, 1982). For example, the increased occurrence of nettles, *Urtica dioica* L., in field margins is ascribed to increased use of fertilizers whereas weeds typical of acid soils, e.g. corn marigold, *Chrysanthemum segetum* L., have declined due to liming (Moore, 1977). The introduction of inorganic fertilizers and pesticides has also been influential in changing farming practices as they have removed the need for crop rotation as a means of maintaining soil nitrogen levels and controlling pests populations (Lloyd & Wibberley, 1977). This has lead the way to increased monocropping, especially of cereals. In the 1970's the latest change in husbandry was towards minimal tillage where subsequent crops were drilled directly into the stubble without ploughing (Cannell & Ellis, 1972). The justification for this change was to save monetary inputs through reduced fuel and labour costs and also to minimise the time required for cultivations (Gibbard *et al.*, 1989). This practice has, however, also influenced the arable weed flora. For example, increased use of minimum tillage has been documented as having favoured the grass weed *Bromus sterilis* which has increased in abundance since this practice became popular (Anon, 1981).

Improvements in seed cleaning techniques have also affected the abundance of those weed species that persisted as a consequence of being annually resown with the crop. The rapid decline of corncockle, *Agrostemma githago* L. has been attributed to these developments (Salisbury, 1961). 22% of the British flora relies on agricultural land as its major habitat and of these species 10% are now declining in number (Ratcliffe, 1977). Some species with diminishing abundance whose main habitat is cultivated land include *Ranunculus arvensis* L., *Papaver rhoeas* L., *Euphorbia platyphyllos* L. and *Torilis arvensis* (Huds.) Link (Ratcliffe, 1977). The threatened loss of such species has lead to increased calls for their protection by conservationists.

The recent government policy of "set aside" provides some hope for potential sites for agricultural weeds to re-establish themselves despite being limited by the strict management criteria imposed. The scheme is designed to curb over production by subsidising farmers to remove land from arable production for limited periods of time. Management of set aside land is restricted, the land can be left fallow, sown with grass mixtures, grazed by non productive livestock, e.g. horses, or "topped" i.e. mown to leave a 10 cm stubble. Use for non agricultural purposes, e.g. caravans, camping, is also permitted Control of the vegetation by herbicides is limited, only non-residual herbicides are allowed is certain circumstances (Carter, 1989). Land that is set aside tends to be the poor quality arable land or field headlands which were low yielding anyway (R. Naden pers. comm.).

More promising still is the scheme of conservation headlands, being promoted by the Game Conservancy Trust, primarily for the establishment of partridge populations (Potts, 1990; Sotherton, 1990). However, in developing environments suitable for partridges it is necessary to support their insect diet and consequently, the flora on which this feeds. Simple management strategies are suggested that involve the reduction of herbicide and pesticide applications to headland areas therefore favouring the traditional flora and fauna. Although primarily aimed at supporting game in this country, the principle of conservation headlands mainly for plants has been used with success in Germany (Eggers, 1987).

1.3 Rarity

One of the aims of the conservation movement today is the preservation of rare species. Which species classify as rare, however, depends not only on the species abundance but also on the scale of investigation and political boundaries (Harper, 1981). Rabinowitz (1981) clarified the concept of rarity. She stated that, conceptually, all forms of rarity can be defined considering three characteristics of a species, namely the geographic range, habitat specificity and local population size. For a particular *species if* any of these characteristics is restricted then the species can be considered rare, i.e. a species with a narrow geographic range, very particular habitat requirements or small local populations.

Rarity can be a phenomena in both time and space (Harper, 1981), plant populations fluctuate between years, or over longer periods, as well as geographically. Spatially rare species can either be scarce, never existing as large populations, e.g. Deptford Pink, *Dianthus armaria* L., in North America (Rabinowitz, 1981) or existing as a few locally abundant populations, e.g. Fritillaries, *Fritillaria meleagris* L., in Britain.

Spatial rarity is dependent on several features mainly the existence of habitable sites, their size, number, temporal availability and carrying capacity as well as the dispersal ability of the plant (Harper, 1981). Regardless of scale any environment can be considered as a patchwork of habitable sites (Gadgil, 1971). A habitable site is the section of the patchwork that can support an individual species through its life cycle, it is an area that possesses the conditions and resources to permit establishment, growth and reproduction of the species in question. Therefore habitable sites are species specific, different species having different requirements although overlap can be extensive. The existence, size and number of these habitable sites, therefore, directly controls the potential abundance of a species. If only a few, small sites exist a species will remain rare.

The temporal availability of habitable sites is also important. Natural succession or disturbance occurring within a site may limit its suitability. Habitable sites can be lost to a species by a competitively superior species excluding the rarity or colonisation by other species blocking its establishment. If habitable sites are transitory a species may be limited. This emphasises the influence of dispersal ability on abundance as it stresses the importance of propagules reaching the habitable sites whilst they are available. Manipulations of species abundance can be achieved by altering one of these factors.

The changes in agriculture in the United Kingdom over the last fifty years have resulted in the degradation and removal of habitable sites for some species, hence the decline of these species (Ratcliffe, 1977). For example, the reduction in numbers of Viper's grass, *Scorzonera humilis* L. is thought to be due to the ploughing up of damp grasslands where it used to be found (Perring, 1970).

Arable weeds that are rare tend to be those with narrow habitat specificities as they have evolved to survive under the "unnatural" patterns of disturbance experienced in an agroecosystem. The removal of their habitable sites, therefore, has an acute affect on the species abundance. The implication for conservation is the need to create habitable sites within the agroecosystem in which rare weeds can maintain populations. To be acceptable to farmers these populations would have to present little threat of infestations that could damage the crop. As such the idea of the conservation headland is acceptable from both points of view.

1.4 The scientific basis of conservation.

The science behind conservation today is an amalgamation of three areas of biology namely autecology, genetics and population ecology (Simberloff, 1988). Early approaches to conservation relied on a knowledge of the autecology, especially the habitat requirements, of a species to plan the management of reserves (Cox, 1974; Owen,1975).

Conservation science has now developed, via the island biogeography theory (MacArthur & Wilson, 1967) to include considerations of the genetics and population ecology of threatened and conserved species (Simberloff, 1988). This has lead to the development of the concept of a minimum viable population, MVP, "the minimum number of individuals in a population needed to guarantee a high probability of survival" (Soulé & Simberloff, 1986). The factors that control the MVP, for any given species, can be categorised as either intrinsic or extrinsic. Intrinsic considerations include genetic factors such as inbreeding depression and genetic drift. Extrinsic considerations include factors regulating population numbers, for example, predation, interspecific competition and disease as well as physical peturbations in the environment, e.g. hurricanes, floods, fires (Soulé & Simberloff, 1986).

One of the areas of debate in conservation science has been over the optimal size of nature reserves, summarised by the acronym SLOSS (Single Large Or Several Small) (Simberloff, 1988). The equilibrium theory of island biogeography indicated that a single large reserve would contain more species than the same area divided into small reserves (Diamond, 1975; 1976; Diamond & May, 1976). This assertion has since been criticised (Simberloff & Abele, 1976a, b). The argument has now been resolved, theoretically, with the conclusion that the equilibrium theory is neutral on the issue of SLOSS (Gilpin & Diamond, 1980; Higgs, 1981). However, discussion still continues as to the benefits, in terms of minimisation of the effects of catastrophes on overall species number, of small reserves compared with the disadvantages of having small populations which are more sensitive to such catastrophes. In general, subdivision appears to be preferable but only to a critical level determined by the MVP of the species targetted for conservation (Soulé & Simberloff, 1986). Connection of small habitat refuges by "corridors" of protected habitat has also been recommended (Simberloff, 1986) in considerations of refuge design. Immigration, facilitated by corridors, from other reserves may stem inbreeding depression and permit natural reintroduction of a species lost as a result of natural catastrophes. However, there is the risk of corridors being a disadvantage in terms of the spread of disease and predators amongst reserves (Simberloff, 1988).

Effective attempts to conserve species require a detailed knowledge of the autecology of the species concerned and the use of appropriate population genetics and dynamics models (Burgman *et al.*, 1988). Conservation of an individual animal or plant species, or community, also requires active management, due to the dynamic nature of populations and their habitats, not just protection from the detrimental influences of man (Stone, 1965).

1.5 The arable ecosystem as a habitat mosaic.

If the field headland is to be considered as a potential habitat for the conservation of rare arable plants, as has been made feasible by the concept of conservation headlands proposed by the Game Conservancy Trust, information on the characteristics of such a habitat is also essential. On an anthropocentric scale the arable ecosystem can also be considered as a mosaic of different habitat types. This mosaic consists of three main components, each with its own characteristics, namely the crop, the headland and the field margin with associated communities of coppices and woods.

The cropped area is a theoretically, and often in practice, homogeneous environment supporting a monoculture. This area is subjected to regular peturbations on an annual basis. The major disturbances occur at the stages of seed bed preparation and harvest. During seed bed preparation ploughing, harrowing and seed drilling disturb the soil to various depths, depending on the practice and implement. At harvest all plant material above the height of the cutter bar is cut and threshed, the bulk of the material being deposited from the combine onto the stubble surface where it is subsequently burnt or removed. Other peturbations of a less physical, but nonetheless influential, nature include applications of fertilizers and pesticides.

The headland is also heavily influenced by husbandry but experiences greater variability in forms of disturbance especially crop sowing density and chemical applications. In the strictest sense the headland is the area of a field where farm machinery turns and only extends as far into the field as this turning circle (Greaves & Marshall, 1987). Therefore a larger proportion of this area experiences compaction due to vehicles, further adding to its unpredictable nature.

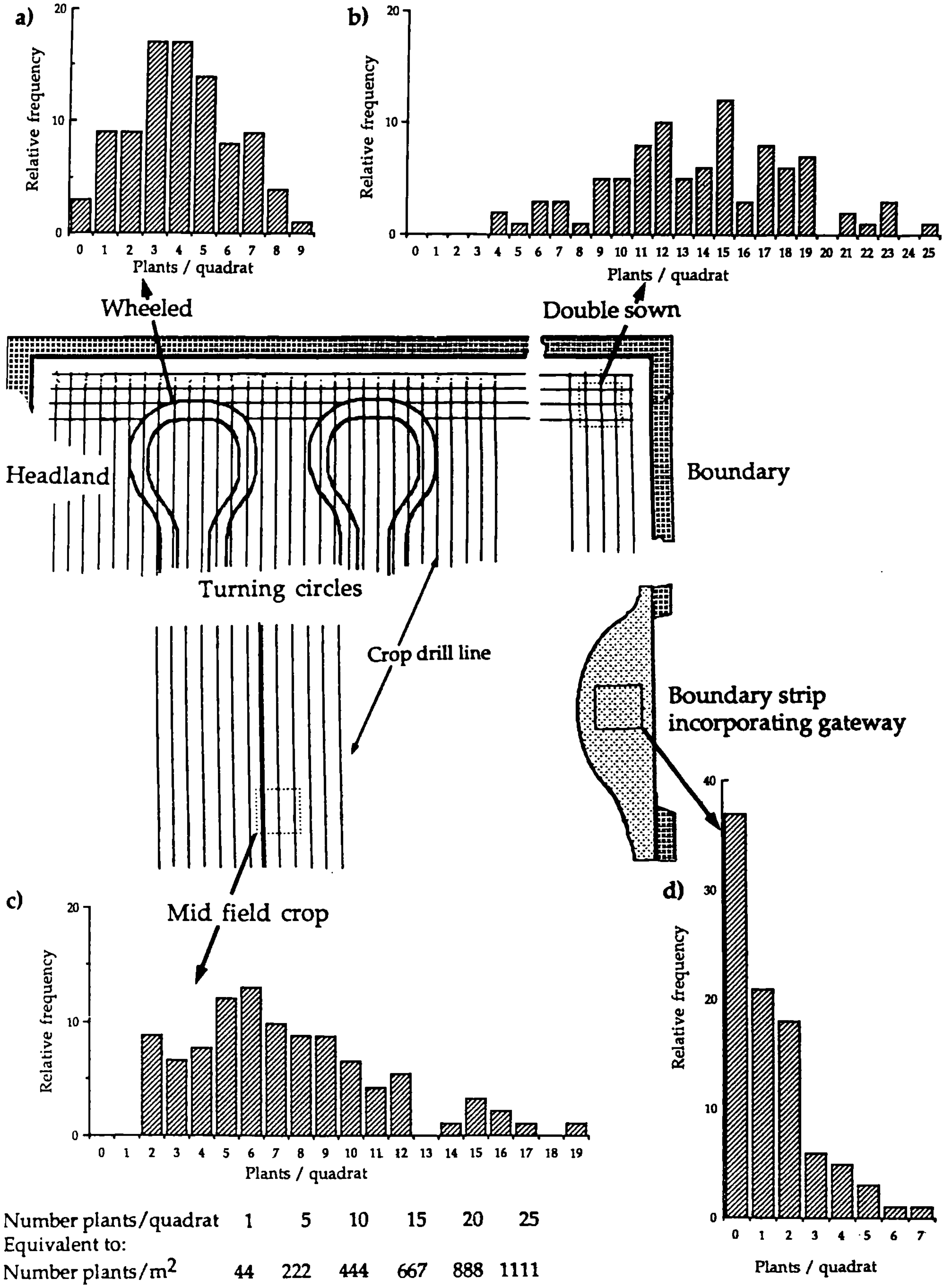
The field margin, often represented by a hedge or a ditch, is also managed although less intensively than the two other elements of the agroecosystem mosaic. Field margins frequently comprise mixed communities of annuals, perennials, shrubs and trees (Greaves & Marshall, 1987). They also represent links between the remaining woodlands and coppices that still exist within the agricultural landscape. As such they can facilitate the movement of wildlife between such areas (Marshall & Smith, 1987) which is regarded as benefical to small isolated populations (section 1.4). Although some species may use such "corridors" woodland species of plants have been found not to disperse along these links (Helliwell, 1975). Hedgerows are commonly thought to act as a reservoir for crop weeds but the majority of species found within the hedge are rare within the cropped area (Marshall & Smith, 1987).

The mosaics that comprise the agroecosystem of today are a direct result of the past and present agricultural management and the associated floras of crop and field margins demonstrate the powerful forces of interspecific selection such management practices exert (Haas & Streibig, 1982).

Figure 1.5.1 illustrates the idea of an arable field as a habitat mosaic and the histograms, **a** - **d**, demonstrate the range of variation that can exist in just one element, the crop density, of the mosaic. The headland contains potentially greater variation in crop density as it consists of areas represented by the three histograms **a**, **b** and **d**. The occurrence of vehicle pressure, where the farm implements turned, was sufficient to reduce seedling numbers from an average of 326 m^{-2} to 180 m^{-2}. Comparing histograms **a** and **c** it can be seen that not only is the mean reduced but also the range of densities recorded. The presence of a gateway created an area of greatly reduced wheat density, with a mean of 57 plants m^{-2}. This area also comprised a high proportion of bare ground, histogram **d**. The headland also contains areas of higher than standard density where double sowing has occurred, histogram **b**. In such areas of double sowing a mean density of 612 plants m^{-2} was recorded. There are even variations apparent in the supposedly homogeneous area of the main crop. The small second peak seen on histogram **c** corresponds to twice the average crop density and is due to the occasional overlap of drill lines that occurs.

The exact area of any headland represented by each of these elements of the mosaic depends crucially on the sowing pattern, which itself is largely determined by the shape of

Figure 1.5.1 A schematic diagram of an arable field considering one component of the habitat mosaic. The range of crop densities apparent in a survey of a cereal field, conducted in November 1988, are shown in relation to machinery passage and sowing pattern. The density of winter wheat cv Norman, one month after sowing at a rate of 200 kg ha^{-1}, was recorded for 92 quadrats (0.0225m^2) within each of four elements of the mosaic. Definitions follow Greaves & Marshall (1987).



Number plants/quadrat	1	5	10	15	20	25
Equivalent to:						
Number plants/m^2	44	222	444	667	888	1111

the field. Further variations within a field can be created by such physical factors as differences in drainage, the aspects and gradient of the land. The mosaic nature of a field is therefore a more complex pattern than described here.

1.6 The influence of husbandry practices on the growth of weed populations.

The species studied in the work reported in this thesis all reproduce sexually on an annual basis, the persistence of each species over time depending on the production of seeds and their subsequent germination and establishment. For grasses a seed can be regarded as a single caryopsis (van der Pilj, 1982). A plant population will increase in size if the finite rate of increase (or per capita multiplication rate) of the population is greater than unity and, conversely, decline towards extinction if the finite rate of increase is less than unity (Mortimer, 1987). A knowledge of the factors that influence the finite rate of increase of a population is, therefore, useful in developing strategies for the conservation or control of that species. Recent work has indicated the importance of a variety of husbandry practices on the population numbers of weed infestations. For example, the use of herbicides has been shown to reduce the rate of population increase of weeds grown in winter cereals compared to untreated populations (Manlove, 1985; Ulf-Hansen, 1989). Experiments have also shown that the interaction of straw disposal, tillage and herbicide use influenced the long term trends in population numbers of *Alopercus myosuroides* Huds., *Avena fatua* L. and *Stellaria media* L. (Wilson *et al.*, 1989). Straw burning reduced the speed at which population numbers of *A. myosuroides* increased, the reduction being greatest when an application of herbicide controlled the seed production of the reduced number of plants that established from seeds that had survived the straw burning. Ideally, therefore, studies of the population ecology of arable weed species would include such influences in order to gain maximum information on the factors that regulate population numbers in arable situations.

1.7 Thesis objectives

The broad aim of the work reported in this thesis was to identify differences amongst the four brome species that could account for the present variation in their abundances.

Consideration of the possibility of conserving a rare arable weed species necessitates an understanding of the species ability to persist within the arable habitat and also the potential of any introduced population to spread within this habitat. To this end the work reported here divided into three areas:

1) Comparative studies of selected aspects of the autecology of the four brome species considered.
2) Assessment of the population growth of the four brome species in simulated headland conditions.
3) Investigation of the distances of seed dispersal that occurred both naturally and as a result of husbandry practices.

Chapter 2

Autecology

2. Autecology

2.1 Introduction

Autecology is defined as "the study of the individual, or members of a species considered collectively, in relation to environmental conditions" (Hanson, 1962). Autecological studies provide essential information on the life cycle and characteristics of a species without which no plant species can effectively be controlled (Fryer, 1975) or conserved (Burgman *et al.*, 1988). In this chapter four independant studies are reported. Each investigated a key aspect of the life cycle of the brome grasses relevant to their existence in an arable ecosystem.

Annual plant species fall into two categories either those whose life cycle ends with flowering and subsequent seed production or those whose life cycle could theoretically continue beyond flowering but which are terminated by external events, usually adverse climatic conditions (Harper, 1977). The former are said to display a determinate growth form (Wareing & Phillips, 1981), characterised by a vegetative growth phase followed by a flowering phase where the main meristem becomes an inflorescence hence precluding any further vegetative growth. The alternative, the indeterminate growth form, is characterised by simultaneous vegetative growth and flowering. The determinate growth form is typical of arable weeds and Mediterranean annual grasses where the species are adapted to seasonal events, in these two cases disturbance at harvest and during periods of drought respectively. In determinate species, the change from the vegetative growth phase to the reproductive phase is usually controlled by the photoperiod experienced by the plant.

One of the characteristics associated with the indeterminate growth form is that flowering and seed set usually occur within a relatively short time from establishment and continue as long as conditions remain favourable (Harper, 1977). This enables maximal exploitation of long, undisturbed growing seasons whilst ensuring some seed production even under adverse conditions (Harper, 1977). However in ecosystems subject to temporally predictable distubances this plasticity of response is unnecessary.

2.1.1 Seed dissemination and dispersal.

Flowering and subsequent seed set precede the dissemination and dispersal of seeds. Most studies of the dispersal of seed have concentrated on the distances seeds move from source (see Chapter 4). Few have looked at the ecological importance of the timing of seed dispersal (Harper, 1977). Plants not only vary in the time at which their seeds ripen but also in the lengths of time ripe seeds remain on the plant. For example, two pines, *Pinus radiata* and *P. cembra*, have been recorded with viable seeds retained within cones for upto 5 years (Fielding, 1965). Conversely, many plants shed the majority of their seeds within days of maturity being reached e.g *Papaver rhoeas* L. (Harper, 1966).

There are three broad patterns of seed release 1) seeds released as ripened, 2) seeds retained on the plant and released in a sudden flush and finally 3) seeds released slowly over time (Harper, 1977). Indeterminate species tend to display the first pattern releasing their seeds as they ripen throughout the growth season. For determinate species both the latter patterns apply.

For species with little or no innate seed dormancy prolonged dissemination in a temporally heterogeneous habitat increases the probability of some fraction of the seed germinating in suitable conditions. The domestication of plants has tended to result in selection for the prolonged retention of seeds, to enable harvesting by man, clearly indicating the genetic control of dissemination (Harper, 1977). Some arable weeds have adapted so closely to harvesting patterns that they now rely on the harvesting process for their dispersal. In the case of *Camelina sativa* (L.) Crantz, which has adapted to be harvested and resown along with flax, the weed has evolved to resemble the flax crop in height, timing of maturity and seed morphology (Sinskaia & Betuzcheva, 1931) thereby ensuring that the weed was harvested with the crop. Retention and release of seeds have different ecological advantages as shown by Harper's (1966) work on poppies. Retention of the seeds in the capsule on the plant by *Papaver argemone* L. facilitate its contamination of the crop at harvest with the benefits of greater dispersal but at the expense of being a favoured food of birds whilst full capsules of seeds are on the plant. In contrast, capsules of

P. rhoaes emptied within a few days of the seed ripening but the species has a limited dispersal range in terms of distance compared to *P. argemone*.

2.1.2 Seed germination strategies.

Angevine & Chabot (1979) divided germination strategies into two categories based on whether the seeds "avoided" or "tolerated" conditions unfavourable for germination. They described the mechanism of tolerance as the product of a high maternal investment, either in the form of vast numbers of seeds or large seeds which provide energy reserves to support the seedling during early growth. Avoidance strategies were subdivided according to the nature of the stress, whether physical i.e. cold, drought, or biotic i.e. due to existing vegetation. Strategies that provided avoidance of biotic factors involved either temporal or spatial dispersal of seeds.

Species that disperse temporally were further subdivided into three categories. The first, fire sensitive, germinate after fire, colonising the exposed soil. The second subdivision, allelochemical substance sensitive, describes species whose seeds are inhibited from germinating by plant derived chemicals released from surrounding vegetation or leaf litter. The final category described by Angevine & Chabot (1979) was that of the "arable weed syndrome" used to describe species that display a group of germination characteristics common amongst arable weeds. These characteristics include seeds that remain dormant while buried, often displaying a light requirement for germination, germination that is rapid and occurs over a wide range of temperatures.

One of the mechanisms by which temporal dispersal of seeds is achieved is dormancy. According to Cook (1980) "the most important demographic property of all seeds is the variation in their capacity to remain dormant and viable in the soil". The populations of seeds within the soil are referred to as seed banks. The size and longevity of seed populations in the soil form a spectrum of patterns, the extremes of which can be described in two categories, those that form persistent seed banks and those that have only a transient seed bank (Grime, 1979). A persistent seed bank consists of some proportion of the annual seed production which remain viable but ungerminated within the soil profile from year to year. This fraction can represent either a large proportion of the annual production (e.g. *Stellaria media* L.) or only a small fraction (e.g. *Arenaria serpilifolia* L.). Persistence can be for several years e.g. *Chenopodium album* L., 23 % of the seed bank has been shown to be viable after twenty years burial (Maun & Barrett, 1986). The numbers of seeds within the seed bank varies with vegetation type. Disturbed environments tend to have elevated numbers of buried viable seed in comparison to undisturbed communities (Fenner, 1985). An average of 4360 seeds m^{-2} in the top 150 mm was recorded from samples from 64 arable fields in the English midlands (Roberts & Chancellor, 1986).

In the United Kingdom species with short term transient seed banks are those where the majority of the seed population produced in the late summer germinate in the following autumn. These are characteristically but not exclusively annual and perennial grasses from disturbed environments e.g. *Vulpia fasiculata* (Forskal) Samp. Longer transient seed banks are formed by plants that produce seed in the late summer that germinate the following spring e.g. *Polygonum aviculare* L. and *P. persicaria*L. (Fryer & Makepeace, 1978). Transient seed banks are defined as not lasting for more than one year (Grime, 1979).

Germination in each category of seeds is controlled (stimulation or inhibition) by different factors. Frequently the seed of those species that form persistent seed banks experience the inhibition of germination by darkness, as shown by work on *Plantago major* L. (Wesson & Waring, 1969). A continued absence of light can enforce dormancy for prolonged periods. In these cases, germination is triggered by exposure to light brought about through disturbance of the soil, for example by ploughing. Changes in the intensity of fluctuations of diurnal temperature can also stimulate germination in seed buried at depths beyond light penetration (Thompson & Grime, 1978). Damage to an area of the herbage layer above ground may result in enhanced thermal exchange between the soil and air and result in diurnal fluctuations that are perceptible to the seed. However, this stimulant does not affect small seeded species which have an obligatory light requirement for germination due to their inability to emerge from depth.

The ecological advantages of having a persistent seed bank lie in greater stability of population numbers, the seed bank acting as a buffer to fluctuating population numbers caused by adverse conditions and the ability to exploit a temporally heterogeneous environment through staggered germination (Grime, 1979). The seed bank can also act as a buffer to genetic change within a population as seeds present within a persistent seed bank will have originated over several generations (Silvertown, 1987).

Synchronous germination, often controlled by water availability, is characteristically displayed by annuals without a persistent seed bank especially amongst desert and Mediterranean annuals. In these species, germination can often occur over a wide temperature range and independently of photoperiod. The seeds tend to be relatively large and possess little innate dormancy (Grime, 1979). Transient seed banks are characteristic of spring germinators which often display a chilling requirement of between 2°C and 10°C for anything between a few days (e.g. *Impatiens grandulifera* Royle) to a few months (e.g. *Impatiens parviflora* DC.) (Grime, 1979). The benefit of spring, as opposed to winter, germination is in the avoidance of "winter kill" due to prolonged low temperatures and frost damage. Spring germinators can exploit vegetation gaps formed by these causes.

The four species of brome are generally recognised as winter annuals, germination occurring in the autumn followed by seed production in the following summer. Froud-Williams (1983) identified four groups of arable weeds determined by the periodicity of their germination. The groups are those which germinate in the 1) autumn, 2) autumn and spring, 3) spring only and 4) indifferent of the season. In an arable ecosystem species tend to be favoured whose germination patterns coincide with those of the crop within which they grow (Silvertown, 1981).

The timing of seedling emergence is very influential on the future development of an individual within a plant community (Harper & Ross, 1972). Dominance hierarchies have long been studied within both plant monocultures (Koyoma & Kira, 1956; Ross & Harper, 1972; Weiner & Thomas, 1986) and species mixtures (Sagar, 1959; Williams, 1962; White & Harper, 1970; Bazazz & Harper, 1976). These studies found that the survival of an individual plant depended upon its position within the dominance hierarchy. During establishment, initial differences in plant size become magnified as the plant grows. Larger individuals capture a greater proportion of the available resources thereby further enhancing their own growth and suppressing their neighbours. These effects have been described as asymmetric, the effect of the larger plants being disproportionate to their size when competing for resources with smaller neighbours (Weiner & Thomas, 1986). Further studies have shown that, although the three species investigated displayed relatively asymmetric competition, the estimated degree of asymmetry differed amongst the species (Thomas & Weiner, 1989). These differences, they suggested, may be due to species specific differences in allometry and resource allocation as well as differences in resource availability amongst the sites and therefore in the resource competed for.

The influence of environmental factors on seed germination can be complex and subtle. At the scale of a seed, the soil represents a highly heterogeneous medium and for seeds with very specific germination requirements it is the number of suitable or "safe" sites that broadly determines the numbers that germinate. A "safe" site is a position where a seed receives the necessary stimuli to break dormancy, the environmental conditions required for germination to occur and the resources of water and oxygen that are needed (Harper, 1977). The absence of detrimental influences, such as predators and pathogens, are also included in the criteria for a safe site. Studies on *Bromus rigidus* Roth and *B. madritensis* L. (Harper *et al.*, 1965) demonstrated how both the total number of seedlings established and the relative proportions of a mixture were largely determined by the surface "roughness" of the soil, the two species having different germination niches or "safe sites". The two species have different length awns and soil roughness was shown to influence the seed-soil contacts and hence water uptake and germination.

Unsuitable conditions for immediate germination when a dispersed seed first contacts the soil can lead to enforced or induced dormancy. Seeds can display three types of dormancy (Harper, 1957); innate, enforced or induced. Both of the latter types are imposed by environmental conditions, induced dormancy being retained despite the removal of adverse conditions for germination whilst enforced dormancy is lost immediately these adverse conditions are removed. This concept has been developed (Baskin & Baskin, 1987) with the knowledge that buried seeds can undergo phasic changes in the state of dormancy. These changes are caused by conditions within the soil environment, temperature being the main factor involved. Alteration of light intensity, light quality, oxygen and carbon dioxide levels, water potentials and nitrate and nitrite levels can also initiate change in the dormancy state (Baskin & Baskin, 1987).

B. sterilis has been shown to display different types of dormancy depending on the timing of seed collection. Seeds gathered in the field immediately they were mature (often early summer) possessed a short lived innate dormancy which was absent in seeds collected only a few weeks later (Froud-Williams, 1981a). Dormancy can also be enforced in *B. sterilis* by extreme temperatures or lack of moisture (Pollard, 1982). A common trait amongst arable weeds is stimulation of germination by light and inhibition by darkness or far red light but *B. sterilis* has been shown to germinate well in the dark (Grime & Jarvis, 1975). Work on *B. tectorum* L. (Hulbert, 1955) showed that high light intensity could enforce dormancy and this has been shown to be true for *B. sterilis* also (Pollard, 1982). Reinforcement is essential to maintain this dormancy but it goes some way towards explaining the presence of ungerminated seeds still remaining within the panicle until February (Pollard, 1982). *B. sterilis* is very unusual in that it is sensitive to photoinhibition by the far red, active form of phytochrome and this effect is heightened by moisture and temperature stress (Hilton, 1984).

2.1.3 Aspects of the autecology of the four brome species investigated.

This chapter describes a series of experiments investigating aspects of the autecology of the four bromes. The first experiment involved a study of the germination characteristics of all four brome grasses and winter wheat, cv Avalon, over a range of constant temperatures. *B. sterilis* is known to germinate over a wide range of temperatures (Froud-Williams, 1981a) as is *B. mollis* (Flood, 1986) whilst there is no data in the literature on the germination characteristics of either *B. commutatus* or *B. interruptus*.

The second experiment investigated the influence of water availability on the rates of germination of the four bromes. To simulate rainfall and therefore more natural conditions, water was added periodically to the experimental units resulting in fluctuations in the amount of water present throughout the experiment.

Ploughing has been recognised as an effective control measure for *B. sterilis* (Anon, 1981; Froud-Williams, 1983) due to its limited emergence from depth. Seedling emergence from depth, for all four species, was studied, therefore, in a third experiment. The fourth experiment reported in this chapter compared the germination rates of the species in the field either sown directly onto a stubble surface or at shallow depth in a cultivated soil to investigate the temporal pattern of seed germination, in field conditions.

The fifth experiment reported in this chapter is an investigation of the survival of seedlings under vehicular passage. Throughout an arable field, but particularly in the headland, plants are at risk of disturbance due to vehicle passage from tractors and associated equipment used for spraying herbicides and insecticides or distributing fertilizers. If field headlands are to be considered as potential sites for the maintainance of plant species the response of these species to vehicle pressure must be assessed.

The sixth experiment reported in this chapter investigated the influence of the date of planting on the formation of seed by all four bromes.

In order to know how influential the combine harvesting process would be on the dispersal of the brome species (see Chapter 4) it is necessary to know what proportion of seeds are retained on the plants at the time of harvest. Field observations, from earlier experiments on these species, indicated differences in the rates of dissemination between the species. The final experiment reported in this chapter provided quantative data on the rates of seed dissemination of all four bromes.

2.2 Germination response in relation to temperature.

The aim of the experiment reported here was to investigate the speed of germination of seed of the four brome species over a range of temperatures.

2.2.1 Materials and Methods

Twenty seeds of each species were placed in separate 90 mm Petri dishes which contained 50 g dry, sieved soil collected from the field site at Liverpool University Botanic Gardens, Ness, Wirral. 25 cm^3 of distilled water were added to each Petri dish 12 hours before sowing. The dishes were then covered with lids, placed in the dark, in growth chambers at the following controlled temperatures; 0, 12, 20 and 25°C ± 1 °C. Five replicate sowings were placed at each temperature.

The temperature and the number of seedlings that had germinated were monitored and recorded on a daily basis. Germination was considered to have occurred when the coleoptile reached 5 mm in length. After scoring, seedlings were removed. Once the majority of seeds, more than 60 %, had germinated the frequency of monitoring was reduced to every second day and continued for 8 days. Thereafter only the Petri dishes at 0 °C were monitored at weekly intervals.

2.2.2 Analysis

Median Response Time, MRT, the time to 50 % germination of the final number of seeds germinated, "provides a measure of location for non normally distributed data that is analogous to the mean of a normal distribution" (Scott *et al.*, 1984). This statistic was used for descriptive purposes and the analysis of variance performed on the final number of seeds germinated, after 13 days (SAS, 1985). Mean squares, as quoted in Table 2.2.b, are calculated from Type III sums of squares for all analyses of variance reported in this thesis.

2.2.3 Results

Analysis of variance of the number of seeds that had germinated after 13 days indicated significant differences amongst treatments and species ($P<0.0001$ and $P<0.0001$

respectively). A significant interaction was also detected ($P<0.0001$) indicating that the species had responded differently to temperature.

The numbers of wheat grains that had germinated by 13 days declined significantly as temperature increased but above 12 °C germination rate was reduced rather than germination having been inhibited completely. For *B. commutatus* the numbers germinated at 25 °C were significantly lower than at either 12 or 20 °C which indicated that, like the wheat, the germination rate was reduced at the highest temperature. *B. interruptus* and *B. sterilis* showed no significant differences between treatments after 13 days. Anomalously *B. mollis* was significantly lower at 20 °C compared to 12 °C, the differences between 12 and 25 °C not being significant.

As shown in Figure 2.2.1, the species displayed different germination patterns in relation to temperature. With the exception of *B. interruptus,* all the species showed reduction in germination rate at the highest temperature of 25 °C. For both *B. commutatus* and wheat this effect was marked and the final numbers of seed germinated at the end of the experiment were considerably lower than at the other temperatures.

Although initial germination of seed at 12 °C was delayed, MRT values for all the bromes at 12 °C were 2 days higher than at 20 °C, the final numbers germinated were comparable. In wheat, MRT was lower at 12 °C and the final numbers germinated far higher than at either 20 or 25 °C.

For *B. interruptus* the speed of germination increased with the increased temperature, the majority of the seeds germinating within a 24 hour period for each of the two lowest temperature treatments.

Germination, of all four species, was recorded to have occurred at 0 °C after 50 days.

2.2.4 Discussion

Temperature may be a key environmental factor controlling germination in weed seeds (Baskin & Baskin, 1971; 1987). However, several brome species have been shown to germinate over a wide range of temperatures. In tests *B. tectorum* germinated over a temperature range from 10-30 °C (Hulbert, 1955). *B. sterilis* displayed sensitivity to

Table 2.2.a Median Response Times (days) for the four brome grasses and winter wheat at three temperatures.

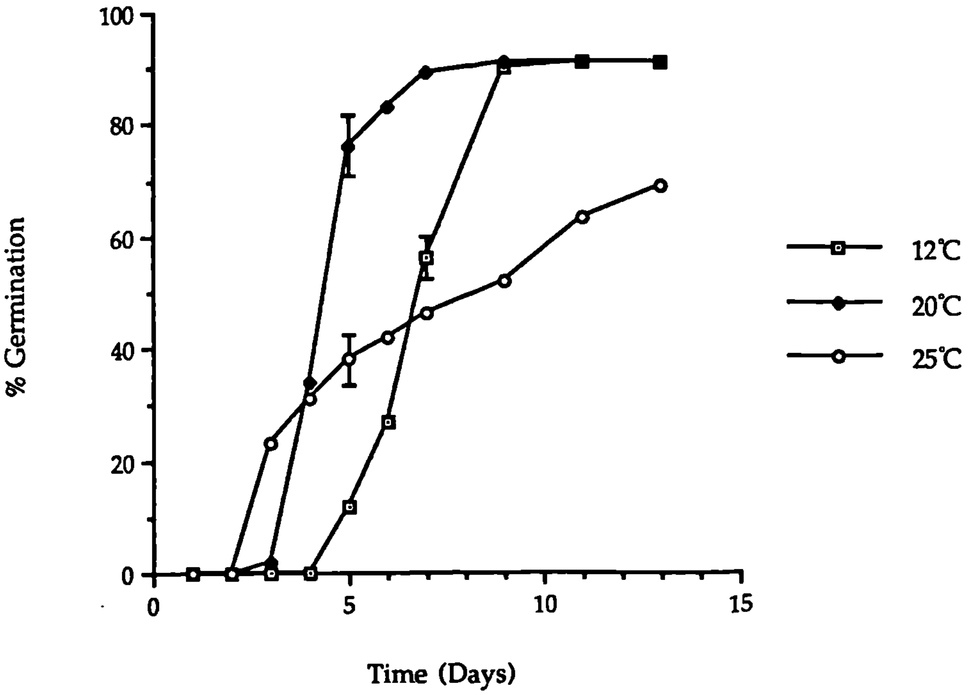
	Median Response Time		
	Temperature		
Species	12 °C	20 °C	25 °C
B. commutatus	7	5	5
B. interruptus	6	4	3
B. mollis	6	4	4
B. sterilis	7	5	4
Triticum aestivum (cv Avalon)	6	7	9

Table 2.2.b Analysis of variance of the numbers of seeds germinated after 13 days under the three temperature treatments of 12, 20 and 25 °C. Type III sums of squares used.

Source	**d.f.**	**M.S.**	**F Ratio**	$P_{(Ho)}$
Temperature (Temp)	2	59.30	17.47	0.0001
Species	4	39.15	11.54	0.0001
Temp. x Species	8	20.64	6.08	0.0001
Error	60	3.39	3.39	
Total	74	8.70		

Figure 2.2.1 Germination of the four brome species and winter wheat, cv Avalon, at three temperatures. Each data point represents the mean value of five replicates. Error bars (± Standard Error of the Mean) are plotted at the first point above MRT.

a) *B. commutatus*



b) *B. interruptus*

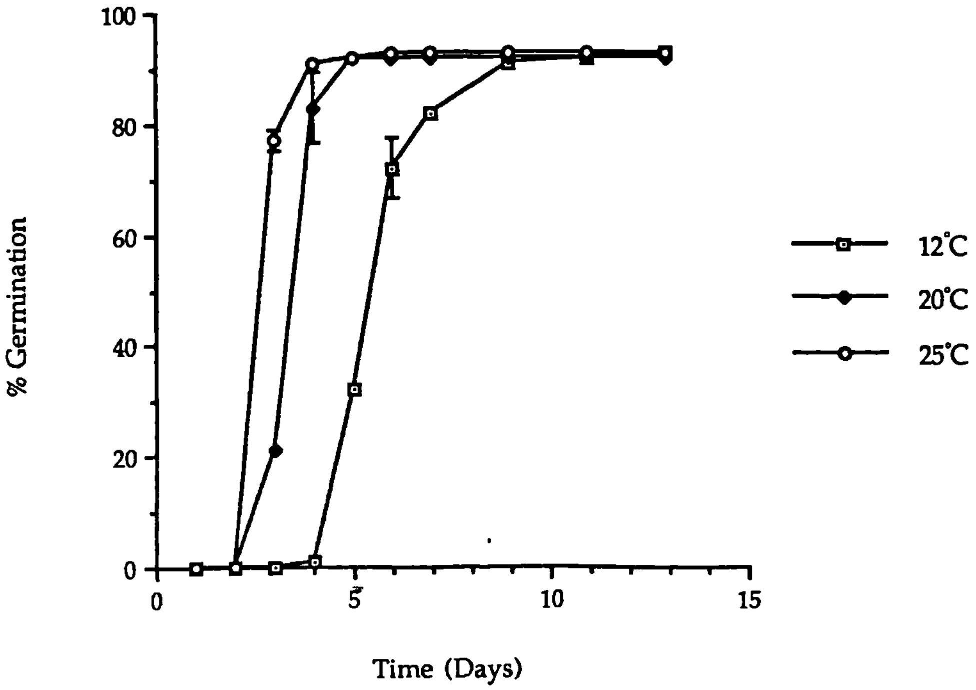
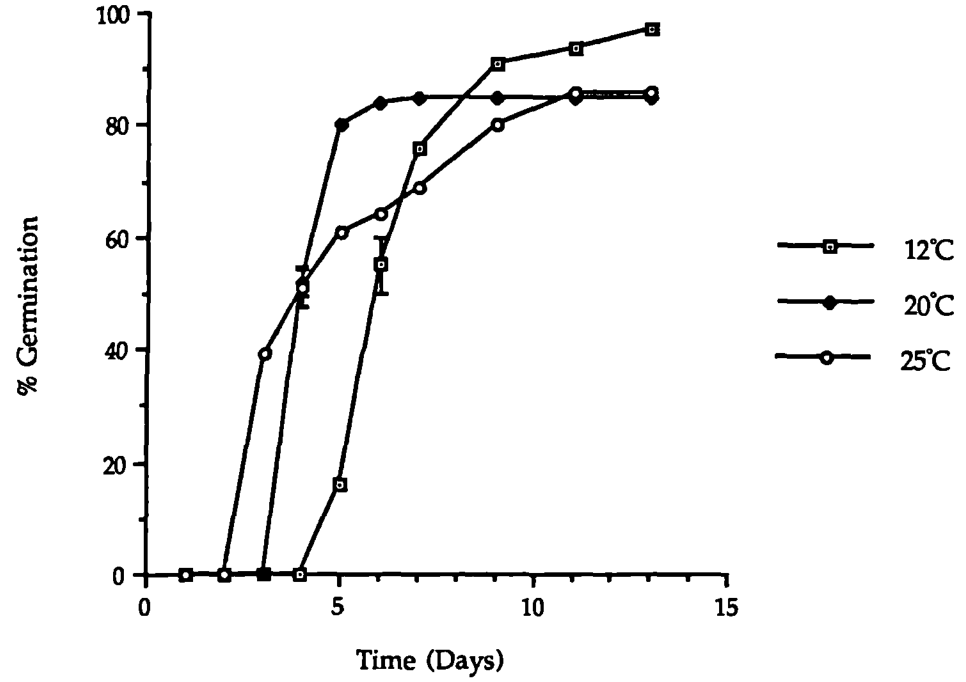


Figure 2.2.1 continued.

c) *B. mollis*



d) *B. sterilis*

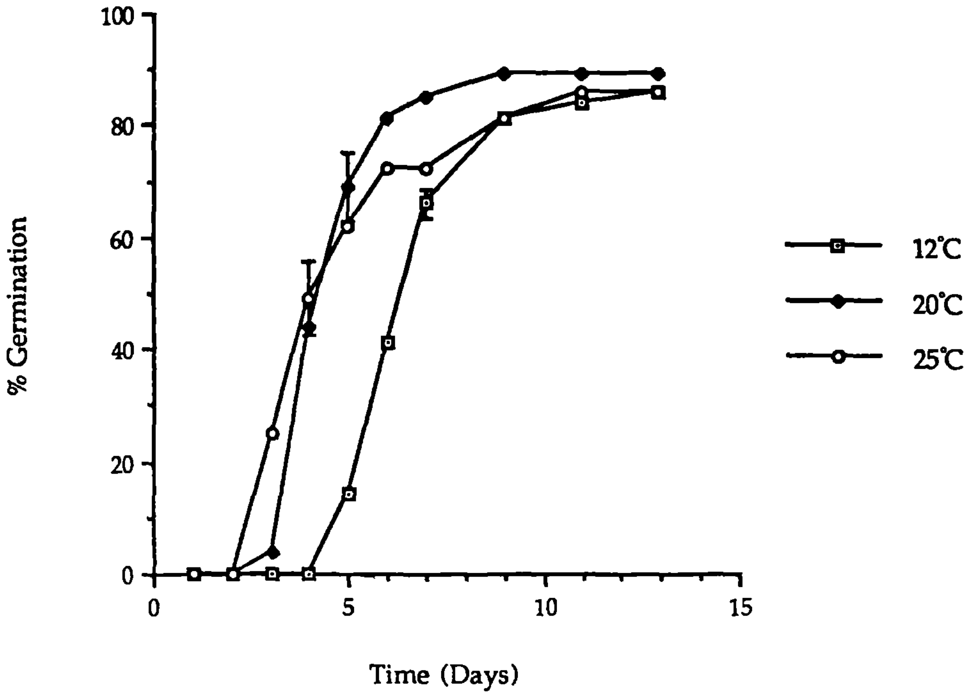
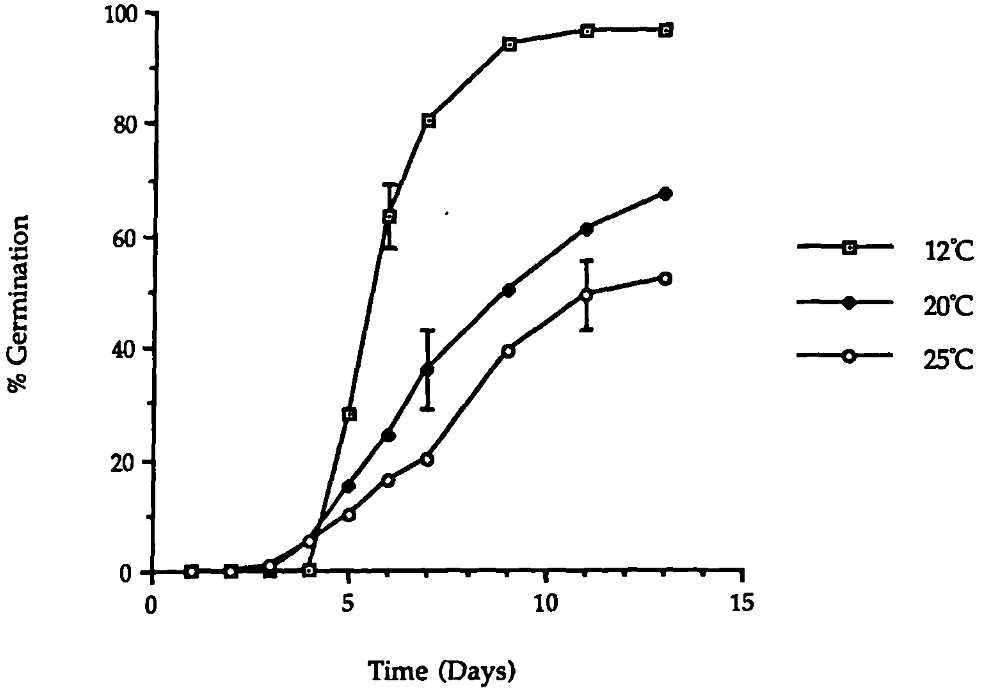


Figure 2.2.1 continued.

e) Winter wheat cv Avalon



temperature for June collected seeds, these having an optima at 10-12 °C where as July collected seeds showed less pronounced variations in germination with temperature (Froud-Williams, 1981a). *B. mollis* has been shown to display maximum germination at temperatures between 10-30 °C, with slower germination at 7 °C. At 35 °C germination was slowed and the final numbers germinated reduced whilst at 38 °C dormancy was enforced (Flood, 1986).

Both *B. mollis* and *B. sterilis* have been shown to germinate at slow rates at low temperatures, *B. sterilis* taking four months to achieve 100 % germination at -2 °C (Froud-Williams, 1981). This effect was also noted by Okereke *et al.* (1981) who recorded 95 % germination of *B. sterilis* at 5 °C after four weeks. Hilton (1984) recorded the germination of *B. sterilis* in darkness as being delayed at both low, 4.5 °C, and high, greater than 23 °C, temperatures with the highest temperature of 28.5 °C enforcing dormancy in some of the seeds.

The results reported here support these general findings for *B. mollis* and *B. sterilis*. Both *B. commutatus* and *B. interruptus* showed broadly similar patterns, the main difference between these two being that *B. commutatus* displayed a markedly slower rate of germination at the highest temperature of 25 °C. *B. interruptus* showed the fastest germination of all the four species, the rates increasing with temperature and at the two highest temperatures, 20 and 25 °C, the majority of the seeds germinated within a 24 hour period, 4 and 3 days respectively, from the start of the experiment.

Winter wheat, in contrast to the *B. interruptus*, displayed germination rates inversely related to temperature, the affects of the highest two temperatures was a very marked reduction in the germination rates. This is to be expected in a cultivar bred for sowing in the autumn.

From these results it is clear that although temperature influences the rate of germination of all the four brome species it is only inhibitory at extremes. In the climatic conditions experienced in the U.K., temperature is rarely going to be the factor prohibiting the germination of any of these species with the possible exception of *B. sterilis* which is more sensitive to photoinhibition at extreme temperature, as previously mentioned. The ability to germinate over a wide range of temperatures is a common trait amongst species with only a short term seed bank thereby enabling germination to occur in a range of weather conditions. No chilling requirement was apparent for any of the species as would be expected for autumn germinators whose main recruitment period, from seeds, is in the late summer and early autumn, before the onset of low temperature conditions.

2.3 Germination in response to water availability.

Using sand as a growth medium the germination of seed of all four bromes was investigated under a range of water availabilities.

2.3.1 Materials and Methods

The water regimes consisted of three supply volumes, 1, 2 or 5 cm^3 distilled water applied either frequently (on a daily basis) or occasionally (on a weekly basis), giving a total of six water treatments (Table 2.3.a). These treatments were applied to Petri dishes containing 50 g dry, acid washed, sand with 20 seeds of each of the four species, individually, on the levelled sand surface. After water applications were made, the Petri dishes were covered with lids to reduce evaporation. Each treatment was replicated four times per species. To maximise the speed of germination due to other factors, the experiment was conducted at 20 ^{o}C and in darkness.

Monitoring of germination was on a daily basis, again germination being defined as the production of a coleoptile greater than 5 mm. Seedlings were removed once recorded. The experiment was conducted between 10.3.90 and 6.4.90.

2.3.2 Analysis

The final number of seeds germinated after 27 days was analysed by analysis of variance (SAS, 1985) with L.S.D.'s being calculated to compare species and treatment means.

Data, pooled over replicates from each monitoring, were analysed by SAS PROC LIFETEST (SAS, 1985) to compare the temporal patterns of germination for the four species under each treatment. The data was treated as survivorship data where the initial event was imbibition and the end event germination (Scott *et al.*, 1984). Due to the cessation of the experiment after 27 days the data was censored, i.e. not all seeds had germinated by this time. The most appropriate test for censored survivorship data, in this case, was the log rank test which equally weighted events throughout the time period of the experiment (Pyke & Thompson, 1984).

2.3.3 Results

The four species showed differences in germination capacity after 27 days ($P<0.0001$). *B. interruptus* displayed the highest overall percentage germination, 96%, compared to the other three species which ranged between 80-84 %.

The treatments significantly effected the final numbers of seeds that germinated, both the rate and the volume of water supply being highly significant in their effect ($P<0.0001$ & $P<0.0001$ respectively). Moreover, species responded differently to the treatments as indicated by the significant interaction term in the analysis of variance (Table 2.3.b).

Germination capacity in *B. commutatus* was only reduced significantly at the very lowest water application rate, Low Occasional, but it can be seen (Figure 2.3.1) that the rate of germination in this species declined with the decrease in water availability. *B. interruptus* showed no differences in final numbers germinated and only very slight differences in the speed of germination. With the occasional water supply at the lowest volume, germination was phasic, a second flush of seedlings following the second application of water. This flushing was apparent, but less pronounced, for other treatment/species combinations e.g. Low Occasional for both *B. commutatus* and *B. mollis.*

In *B. mollis* the largest reduction in the germination capacity was at the Low Occasional water level and, as with *B. commutatus,* the germination rates ranked in ascending order of volume of water received per week. This pattern was not as clear in *B. sterilis,* the initial rate of germination in the Medium Frequent treatment was comparable to the other treatments (except Low Occasional) but the germination rate was reduced after the first week when compared to the other treatments.

At the reduced speeds of germination due to limited water availability, germination in *B. commutatus* and *B. mollis* had not ceased at the time of termination of the experiment.

Analysis of the results by PROC LIFETEST provided statistical evidence supporting these apparent differences in the rates of germination. There were significant

Table 2.3.a Summary of the treatments.

Code	Volume of water per week (cm^3)	Volume of weekly water in relation to quantity of dry sand (cm^3/g)
High Frequent	35	1.43
High Occasional	5	0.10
Medium Frequent	14	0.28
Medium Occasional	2	0.04
Low Frequent	7	0.14
Low Occasional	1	0.02

Table 2.3.b Analysis of variance of the numbers of seeds germinated after 27 days under six treatments, varying the interval and quantity of water applications, over a range from 1 cm^3 weekly to 5 cm^3 daily for seeds on a sand medium in Petri dishes. Type III sums of squares used.

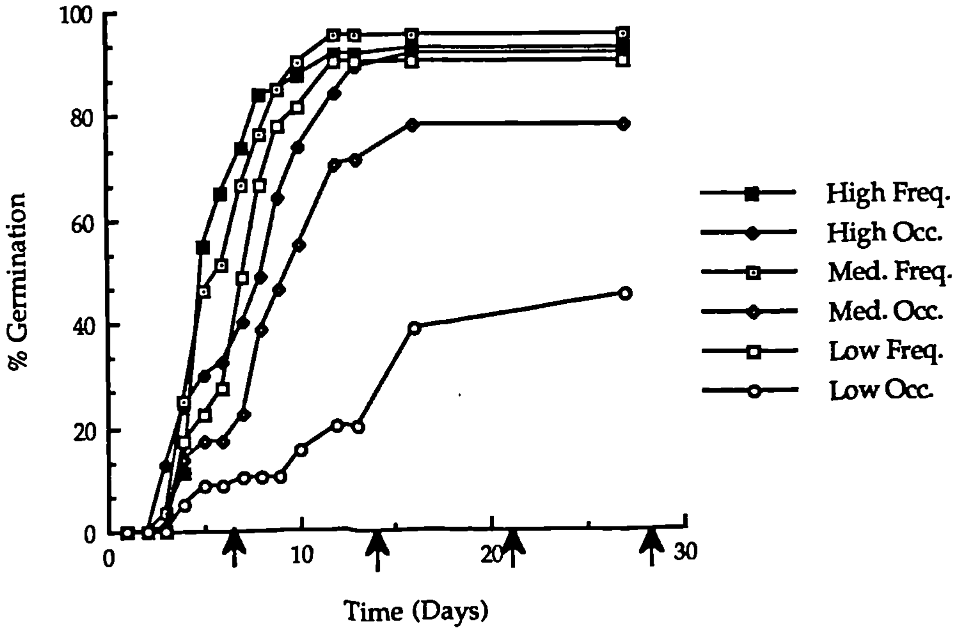
Source	d.f.	M.S.	F Ratio	P(Ho)
Block	3	1.86	0.40	0.7564
Quantity (Quant.)	2	122.17	25.98	0.0001
Interval (Int.)	1	108.38	23.05	0.0001
Species (Spp.)	3	41.31	8.79	0.0001
Quantity x Interval	2	96.13	20.44	0.0001
Interval x Species	6	21.29	9.05	0.0001
Quantity x Species	3	61.78	6.57	0.0001
Int. x Quant. x Spp.	6	25.90	5.51	0.0001
Error	69	4.70	4.70	
Total	95	15.45		

Table 2.3.c Analysis of the temporal patterns of germination of the four brome species at six water availabilities (for treatment codes see Table 2.3.a). Data analysed by SAS PROC LIFETEST (SAS,1985). Chi-squared values quoted are for the Log rank test.

Treatment	**Chi-squared**	**d.f.**	**P**
High Frequent	116.803	3	0.0001
High Occasional	135.325	3	0.0001
Medium Frequent	93.524	3	0.0001
Medium Occasional	147.675	3	0.0001
Low Frequent	127.863	3	0.0001
Low Occasional	65.257	3	0.0001

Figure 2.3.1 Germination of the four brome species under six water regimes. See Table 2.3.a for treatment codes. Each data point represented the mean value of four replicates. Arrows, on horizontal axis, indicate time of weekly water additions.

a) ***B. commutatus***



b) ***B. interruptus***

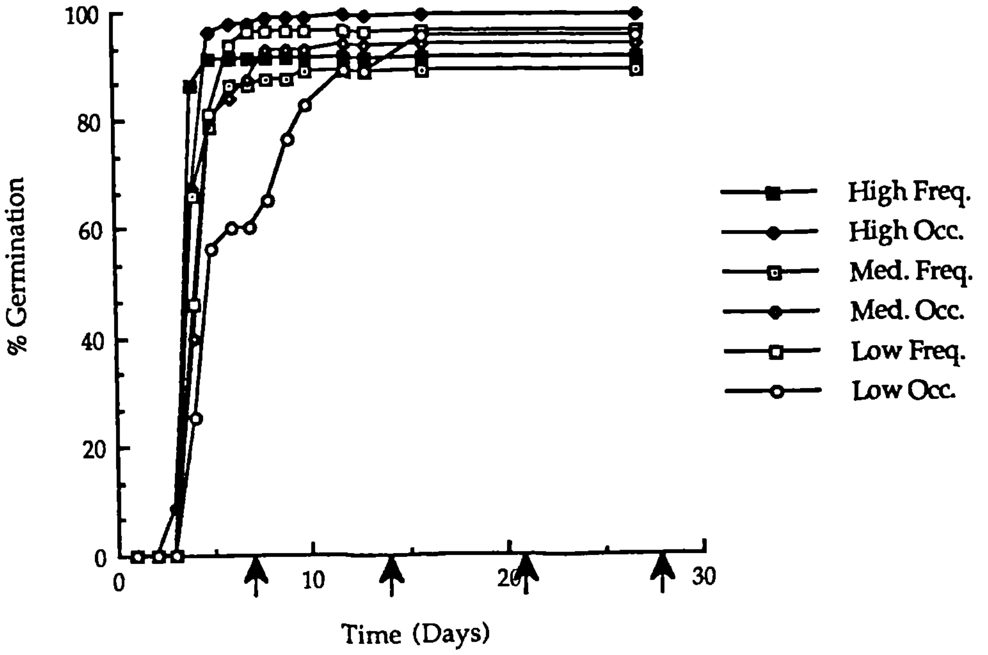
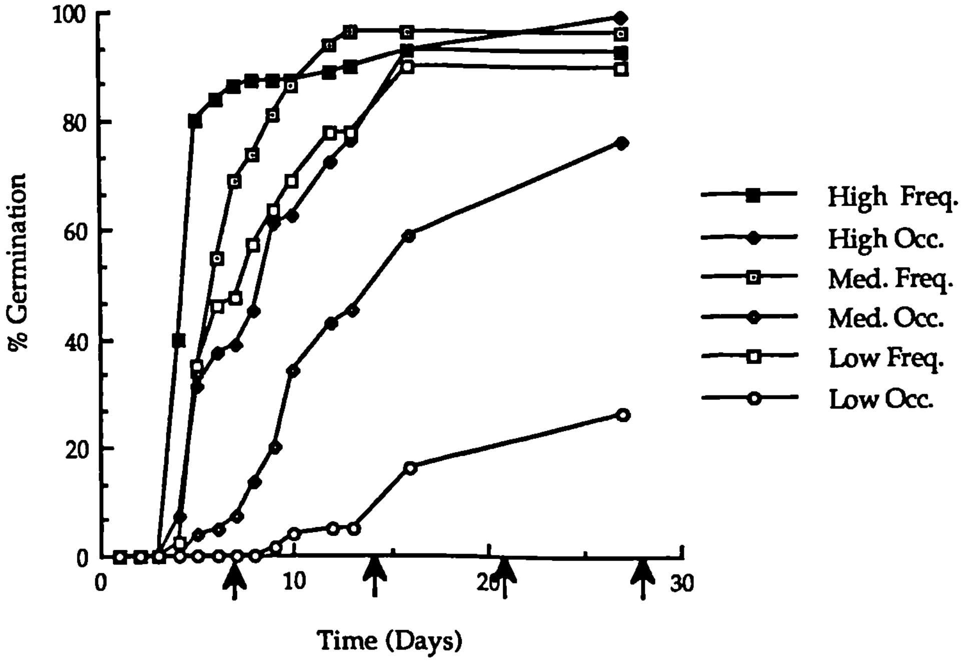


Figure 2.3.1 continued.

c) *B. mollis*



d) *B. sterilis*

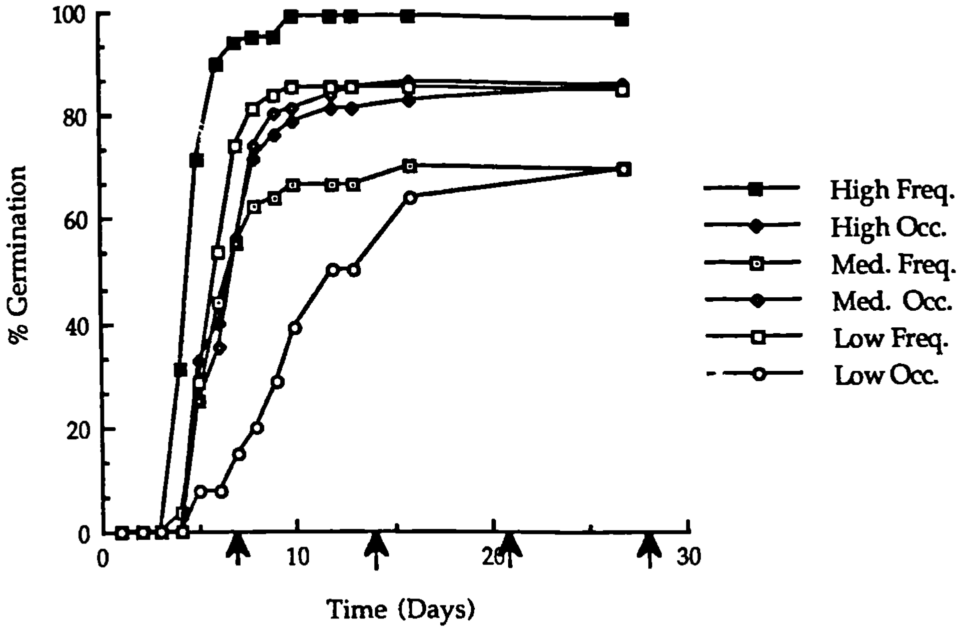
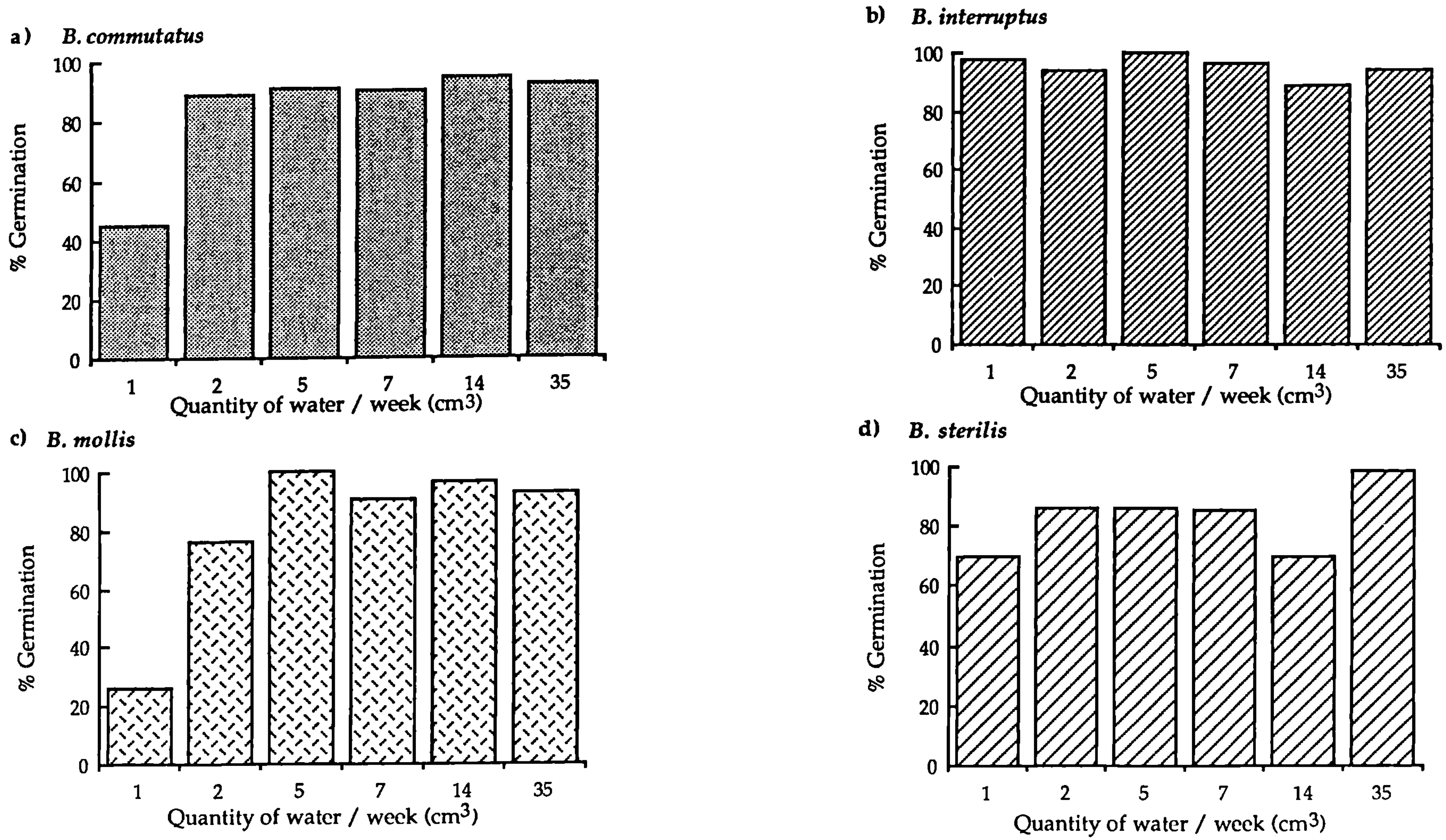


Figure 2.3.2 Mean germination of the four brome grasses, after 27 days, in relation to the quantity of water received per week. LSD $(P < 0.05) = 16.04$.



differences in the rates of germination amongst the species at each of the six treatment levels (Table 2.3.c).

The histograms of the numbers germinated after 27 days emphasise that the total quantity of water received per week dictated the numbers germinated for all species except *B. interruptus*. The interactions between quantity, interval and species were significant due to the marked effect that the Low Occasional treatment had on both the *B. commutatus* and *B. mollis* in comparison with *B. interruptus*, the final germination of both these species being approximately halved with this treatment (Figure 2.3.2).

2.3.4 Discussion

Studies of the influence of water availability on the germination of various species have indicated the importance of seed surface contacts in relation to the speed of water uptake. Larger seeds are reported to have a greater surface area for water loss, relative to the area in contact with the moist surface, than small seeds (Harper & Benton, 1966). Larger seeds are therefore prone to relatively greater loss of water by evaporation and hence require greater uptake to balance these losses and permit germination. An early study (Watt, 1919) on *Quercus* spp. demonstrated how important the soil-seed contacts were where acorns on a level soil surface showed reduced germination compared to those indented or partially buried.

Harper (1977) points out that water availability does not create an "all or nothing" affect on germination. Water stress influences the probability of germination and some species are more sensitive than others as the experiment reported here has clearly demonstrated.

If seed size were the sole influence on germination under water stress, it would be expected that *B. sterilis*, not *B. commutatus* and *B. mollis*, would have been most retarded by lack of water, *B. commutatus* and *B. mollis* being very similar in shape and weight to *B. interruptus* , whilst *B. sterilis* is considerably larger (Table 1.4.a).

The ecological significance of these germination patterns is that seed of *B. interruptus* are capable of rapid and complete germination at very low water availabilities. Although this ability potentially expands the range of environments in which *B. interruptus* can germinate it also has the potential disadvantage of exposing the population of seedlings to dessication if there is no further rainfall. In view of the near synchronous germination shown by *B. interruptus*, at temperatures around 20 °C, this could lead to major losses from the population. Early germination does, however, have the benefit of establishing a competitive advantage over later emerging neighbours. The other species by displaying protracted germination at the low water availabilities have a higher probability of some proportion of their seeds germinating during a period of sufficient moisture for seedling establishment.

Adaptations of desert annuals to the environment in which they live include existing as small plants and displaying fast life cycles (Went, 1948; 1949; Koller, 1969), in some cases as short as six weeks. They also commonly display persistent seed banks to maintain populations during years when reproduction is severely limited by water stress and the ability to reproduce prolifically when unlimited. Only the last of these adaptive features is displayed by *B. interruptus*.

Even though *B. commutatus, B. mollis* and *B. sterilis* show protracted germination at the low water availability there is no evidence in either this or the previously discussed experiment for "somatic polymorphism" in germination requirements. This phenomenon is common amongst ruderals, particularly those with persistent seed banks, as a mechanism for enhancing the probability of germination in suitable conditions and therefore seedling survival. Examples exist where seeds from one plant have different germination requirements (Cavers & Harper, 1966) thereby exploiting different ecological niches within a heterogeneous environment and increased chance of species persistence. Given one set of suitable conditions all four species showed high germination, approaching 100 %, indicating that there is no polymorphism under the set of conditions investigated here.

2.4 Seedling emergence from depth.

The experiment reported here was designed to investigate the emergence of seedlings from seeds sown at differing depths.

2.4.1 Materials and Methods

To investigate seedling emergence from depth, 20 seeds of the four brome species were planted at four different depths in 25 cm diameter pots containing John Innes No 5 compost. Three replicates of each species/depth combination were sown and arranged in a randomized complete block design. The experiment was sown on the 24.2.89.

The planting depths were 10, 50, 100 and 150 mm below the surface. The pots were placed in a polythene tunnel house and watered regularly to ensure sufficient moisture for germination. Monitoring was conducted at weekly intervals for the first five weeks, then two further checks were carried out at three week intervals. At each monitoring, the total number of plants emerged was counted and recorded. The monitoring dates were: 3.3.89, 10.3.89, 17.3.89, 24.3.89, 31.3.89, 19.4.89 and 8.5.89.

After the final monitoring pots were exacavated and examined for the remains of seedlings.

2.4.2 Analysis

The number of seedlings that had emerged after 54 days, after which there was no further emergence, were analysed by analysis of variance (SAS, 1985) (Table 2.4.a).

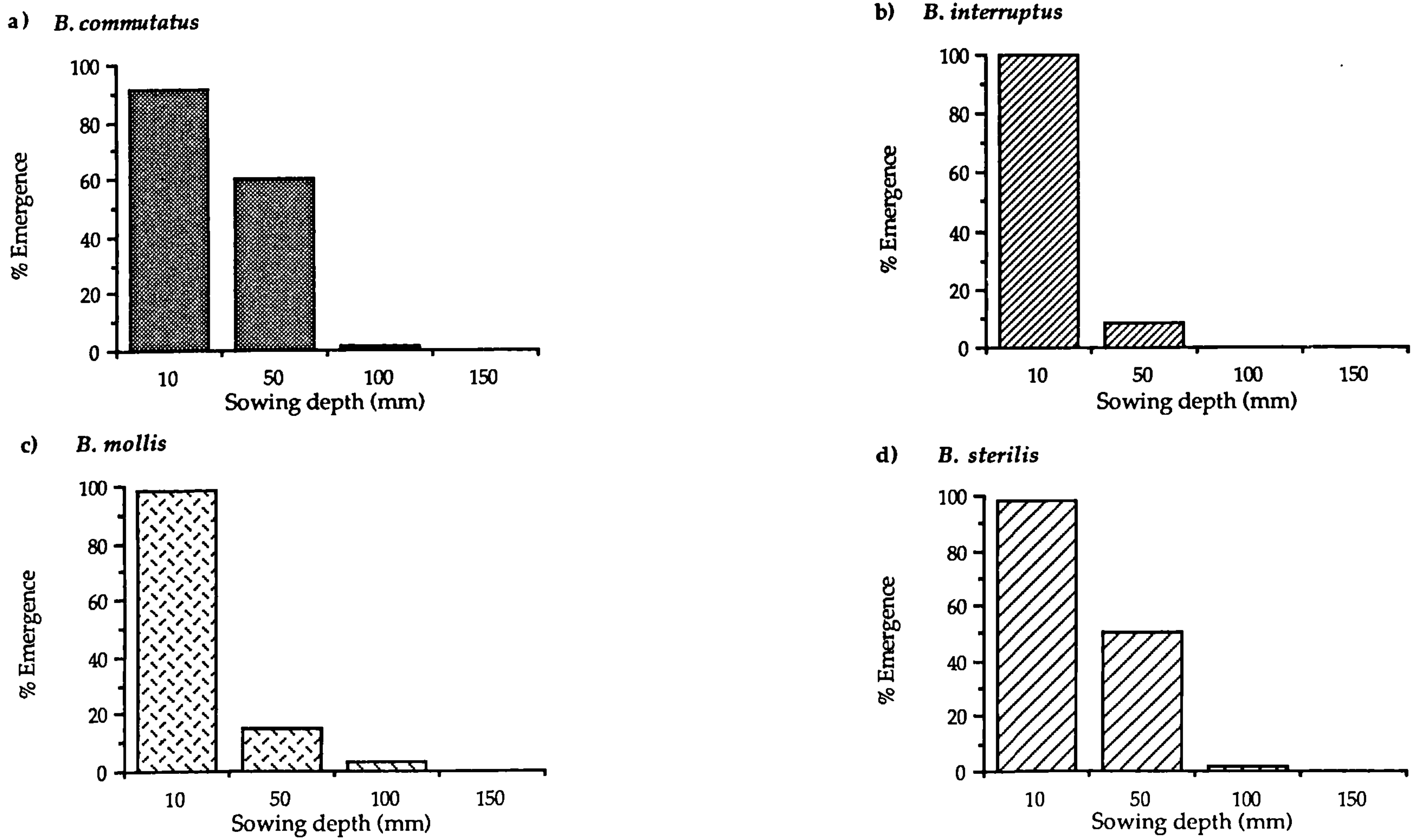
2.4.3 Results

Planting depth had a pronounced effect on emergence ($P < 0.0001$), all four species showing a marked decline in the numbers of seedlings that emerged with increased depth. At a planting depth of 10 mm, all four species showed similar high levels of emergence (all greater than 91 %). In contrast, emergence from 100 mm planting depth was greatly reduced. With the exception of *B. interruptus,* which showed no emergence at this depth, species displayed less than 5 % emergence from 100 mm.

Table 2.4.a Analysis of variance of the number of emerged seedlings, after 54 days, for the four brome species planted at differing depths. Type III sums of squares used (SAS, 1985).

Source	d.f.	M.S.	F Ratio	P(Ho)
Blocks	2	4.34	2.32	0.1155
Depth	3	988.41	59.51	0.0001
Species	3	15.74	8.43	0.0003
Depth x Species	9	21.37	11.45	0.0001
Error	30	1.87	1.87	
Total	47	69.56		

Figure 2.4.1 Emergence of the four brome species when sown at increasing depths, 54 days after planting.
LSD (P < 0.05) = 11.39


a) *B. commutatus*

b) *B. interruptus*

c) *B. mollis*

d) *B. sterilis*

At the deepest planting depth (150 mm) no emergence was recorded for any of the species. On completion of the experiment the pots for this treatment were excavated and it was found that the seeds of all four species had germinated but failed to emerge from this depth.

The species emergence patterns showed significant differences ($P<0.0001$) due to their behaviour at the 50 mm planting depth. The interaction of the depth x species was also highly significant ($P<0.0001$). Both *B. commutatus* and *B. sterilis* showed approximately 50% emergence at this depth whilst *B. interruptus* and *B. mollis* displayed less than or equal to 15% emergence. Although the mean emergence for *B. interruptus* and *B. mollis* differed at this depth by almost a factor of two (8.3 % and 15.0 % respectively) this difference was not statistically significant (L.S.D.=11.39).

2.4.4 Discussion

The above ground population numbers of arable weed species are known to vary under different cultivation regimes, for example blackgrass, *Alopecurus myosuroides* Huds. has been recorded as increasing under minimum tillage regimes whereas chickweed, *Stellaria media* L. and field poppy, *Papaver rhoeas* increased in conditions of more frequent cultivation (Pollard *et al.*, 1982). Populations of *B. sterilis* have become more prevalent since the mid 1970's, these increases following the rise in acreages of winter sown cereals and the adoption of minimum tillage techniques (Cussans, 1976, Froud-Williams *et al.*, 1980). The main reason minimum tillage favours *B. sterilis* is the inability of this grass to emerge from depth (Froud-Williams, 1981b; Gray, 1981).

The results of the experiment reported here support those of other workers who have investigated the emergence of *B. sterilis* from depth. Emergence was found to be severely reduced at 100 mm depth and prohibited at depths greater than this. Froud-Williams (1981b) reported 95 % emergence from a depth of 25 mm but no emergence from 125 mm. He also observed that the seeds buried at depth had germinated but failed to emerge and measured coleoptile extensions of upto a maximum of 120-130 mm. The lack of enforced dormancy by burial was similarly reported by Budd (1981) who measured coleoptile extensions averaging 43.4 mm in germinated, buried seeds.

The other three brome species showed a similar inability to germinate from depths greater than 100 mm, indicating that they also would be controlled by deep ploughing. In the case of *B. interruptus* and *B. mollis,* which both showed severely limited emergence even at 50 mm depth, these species would probably be adequately controlled by shallow cultivations.

The fact that all four species did germinate when buried indicates that none of these species have any light requirements for triggering germination as has been shown to be common among arable weeds (Grime & Jarvis, 1975). Inhibition of germination of seed at depth has the advantage of ensuring seeds only germinate in positions from where they can emerge. Complete eradication of *B. sterilis* infestations by cultural control methods, namely ploughing, has been reported indicating how lethal this method can be (Anon, 1981). From the results reported here this management practice would be expected to have similar, detrimental effects on populations of the other three brome species.

2.5 Germination in field conditions.

The experiment reported here investigated the temporal pattern of germination of seeds of the four brome species both on a stubble surface and at shallow depth in cultivated soil.

2.5.1 Materials and Methods

Fresh bulked seed samples of all four brome species were collected from the field sites at Ness Gardens and were tested for viability using tetrazolium chloride (Moore, 1972).

Seed from these collections were sown in 0.5 x 0.5 m plots of two surface conditions: either a winter wheat stubble cut a week previously, hereafter referred to as stubble, or freshly cultivated soil, hereafter referred to as cultivated. Due to the small size of the plots, cultivation was by a hand operated rotovator. Four destructive harvests were made at fortnightly intervals and each treatment was replicated four times.

The total of 128 plots were arranged in four replicate blocks, on a split plot design. In each block, main plots were surface conditions, sub plots being the harvest number/species combinations which were completely randomised within each split block. The location of main plots were randomised within each block.

The experiment was sown on 7.9.89 and 8.9.89 in warm, dry conditions which were followed by several days intermittent rain (Figure 2.5.2). One hundred seeds were sown evenly within the central 0.1 x 0.1 m of each plot. The diagonal corners of each square were marked by short canes. In the stubble treatment, seeds were sown directly onto the soil surface, whereas on the cultivated soil treatment they were covered to a depth of approximately 5 mm with soil from the surrounding cultivated area. The plots were unprotected so as not to inhibit the likelihood of natural predation occurring.

Harvesting involved relocating the quadrat using the marker canes, then removing and counting all the seedlings within its bounds. Ungerminated seeds were also removed and counted. The four harvests were conducted on 22.9.89, 6.10.89, 20.10.89 and 2.11.89.

2.5.2 Analysis

The number of seeds germinated were corrected for initial non viability on the results of a viability test conducted at the start of the experiment on seed samples from the same collections. The viabilities were found to be as follows;

Species	% Viability	Standard Error
B. commutatus	95	0.71
B. interruptus	100	0
B. mollis	100	0
B. sterilis	86	2.83

Results, corrected for percentage viability, were analysed by analysis of variance (SAS, 1985) (Table 2.5.a), LSD's being calculated for a split plot design (Cochran & Cox, 1957).

The results for the numbers of seeds lost were analysed by analysis of variance (SAS, 1985) (Table 2.5.b). The number of seeds lost was calculated according to the formula:

Number lost = initial number sown (100) - (number germinated + number found ungerminated)

2.5.3 Results

2.5.3.1 Seed germination.

As expected there was a significant difference in the numbers germinated between harvests ($P < 0.0001$). The results clearly showed that the overall germination was greater in the cultivated soil than on the stubble surface. Mean percentage germination, over all species, in the cultivated situation was 74 % compared to only 43 % on the stubble surface. This treatment effect was significant ($P < 0.0001$) (Table 2.5.a).

Under both treatments there were differences amongst the species in the germination patterns ($P < 0.0002$) (Figure 2.5.1.). *B. sterilis* showed greater initial germination under the cultivated treatment than any of the other three species, 67 % compared to 46 % for *B. interruptus*, the second largest, at the first harvest. These differences became less apparent over time as the germination levels approached a

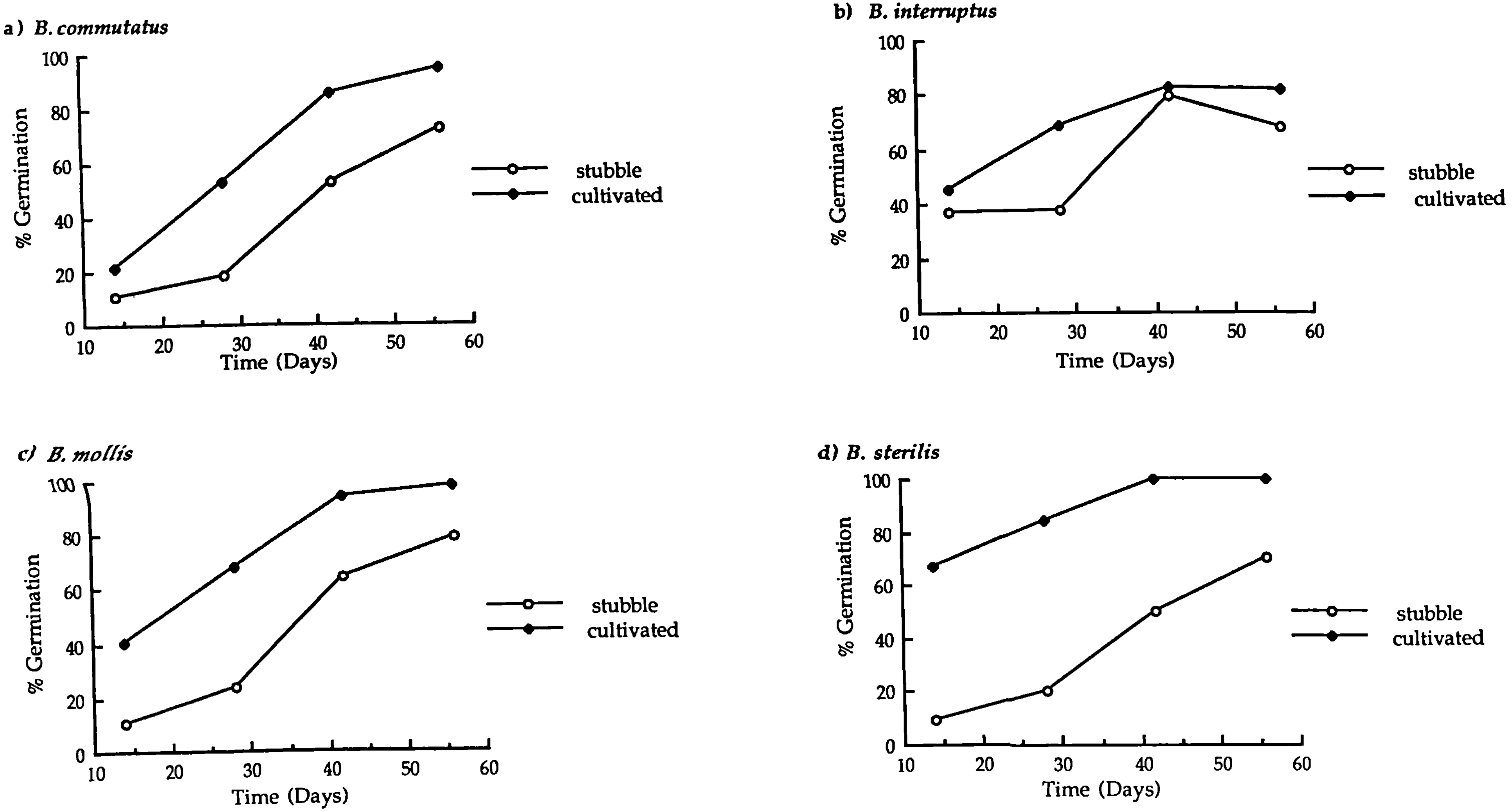
Table 2.5.a Analysis of variance of the numbers of seeds germinated over four harvests, at fortnightly intervals, either on the stubble surface or in cultivated soil. Data corrected for initial non-viability. Type III sums of squares used (SAS,1985).

Source	d.f.	M.S.	F Ratio	P(Ho)
Block	3	153.85	1.10	0.4686
Surface condition(Surf.)	1	29419.31	211.09	0.0007
Main plot error	3	145.24		
Harvest (Harv.)	3	19078.59	158.17	0.0001
Species (Spp.)	3	912.68	7.57	0.0001
Surface x Species	3	1925.73	15.97	0.0001
Surface x Harvest	3	648.13	5.37	0.0019
Species x Harvest	9	355.22	2.95	0.0042
Surf. x Spp. x Harv.	9	153.99	1.28	0.2611
Sub plot error	87	120.62		
Total	124	914.94		

Table 2.5.b Analysis of variance of the number of seeds lost. Data calculated from initial numbers sown minus numbers collected as seedlings and ungerminated seeds. Type III sums of squares used (SAS, 1985).

Source	d.f.	M.S.	F Ratio	P(Ho)
Block	3	44.66	1.16	0.4520
Surface condition (Surf.)	1	1584.00	41.26	0.0076
Main plot error	3	38.39		
Harvest (Harv.)	3	113.54	2.50	0.0647
Species (Spp.)	3	76.71	1.69	0.1751
Surface x Species	3	78.49	1.73	0.1669
Surface x Harvest	3	357.45	7.87	0.0001
Species x Harvest	9	118.19	2.60	0.0104
Surf. x Spp. x Harv.	9	79.74	1.76	0.0883
Sub plot error	87	45.39		
Total	124	75.80		

Figure 2.5.1 Germination, at four harvests, for the four bromes sown either on the stubble surface (stubble) or in cultivated soil (cultivated). LSD (P< 0.05) = 16.24



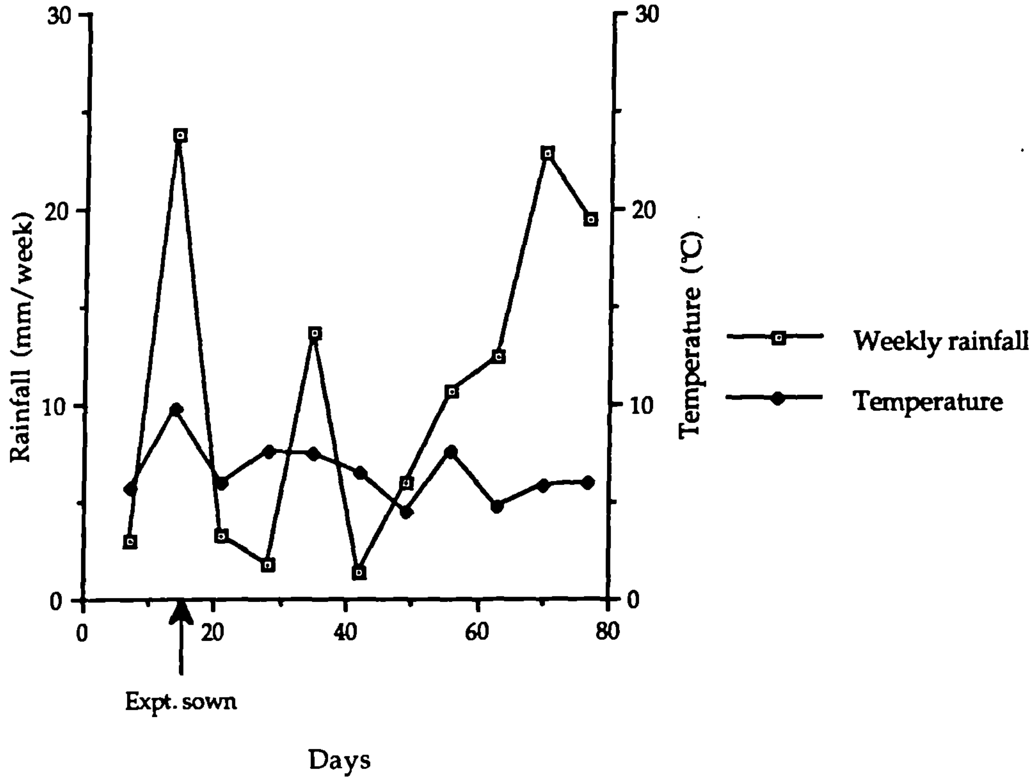
a) *B. commutatus*

b) *B. interruptus*

c) *B. mollis*

d) *B. sterilis*

Figure 2.5.2 Weekly rainfall and average minimum temperature, at grass level, measured at 09 hrs., during the experimental period.



maximum similar for all four species. In the stubble treatment *B. interruptus* showed the highest germination at the first harvest, at a level over 3 times that of the other three species, 37 % compared to approximately 10 % respectively. Again the differences were lost over time. However, the interaction between species and treatment was significant ($P<0.0001$) due to the magnitude of the differences in response. For example, *B. sterilis* exhibited a greater than two fold difference between treatments, over all harvests, whereas for *B. interruptus* at the other end of the response spectrum, the difference between treatments was only a factor of 1.25.

2.5.3.2 Seed loss.

There was a significant difference in the number of seeds lost between the two surface conditions ($P < 0.0001$). The average number of seeds lost from the stubble, over all species and all harvests, was 19.73 compared to only 12.65 from the cultivated plots.

There was no significant differences in seed numbers lost amongst the harvest intervals, species or blocks.

2.5.4 Discussion

Natural precipitation, Figure 2.5.2, during the experimental period was sufficient to allow maximum germination, of all species, on the strength of the findings reported in section 2.3.

The germination patterns of *B. sterilis* on the stubble surface and at shallow depths in cultivated soil has been noted by several authors (Froud-Williams, 1981b, 1983; Gray, 1981; Bulmer, 1987). The results for *B. sterilis* reported here largely support their findings. Froud-Williams (1983) demonstrated germination on the stubble surface to be protracted although 85 % of the seeds had germinated by the end of the first month. However in the experiment reported here only 70 % had germinated on the stubble surface after two months.

Bulmer (1987) showed that incorporation of the seed to a depth of 10 mm accelerated germination of *B. sterilis* and doubled the number of surviving seedlings. A similar promotion of germination was also noticed in response to shallow autumn cultivation (Froud-Williams, 1981b) although a small fraction of the seeds sustained physical damage during cultivation. Reductions in the numbers recorded surviving from surface sowings was explained as the result of higher seedling mortalities rather than the product of enforced dormancy (Froud-Williams, 1983). However other authors point to photoinhibition playing an important role in the persistence of seeds on the stubble surface. Work on *B. tectorum* showed that shading enhanced germination in comparison with seeds on an exposed surface (Young & Evans, 1975). They suggested that shading not only reduced the intensity of irradiation but also altered the wavelengths reaching the seeds. *B. sterilis* may well be sensitive to such changes due to its unusual photoinhibition of germination by far red light.

Various measures of the persistence of *B. sterilis* on the stubble surface have been recorded from 25 % of viable seed persisting for nine months in a non crop situation (Gray, 1981) to 1 % persisting for 12 months (Froud-Williams, 1981b).

B. commutatus and *B. mollis* showed similar responses in surface germination as the *B. sterilis* in that germination was markedly delayed and reduced on the stubble surface. The differences between the treatments shown by these two species were not as great, however, as that shown by *B. sterilis*. On the stubble surface they achieved 73 % and 79 % germination respectively after two months. Only *B. interruptus* showed initial germination on the stubble surface at a level not greatly reduced compared to that in the cultivated situation, indicating that this species may not experience photoinhibition of germination. Without further tests the reasons for the reduced germination rates in *B. commutatus* and *B. mollis* could not be ascertained although it may relate to moisture stress. Burial, even at shallow depths, has the advantage of providing some protection from dessication and also greater seed-soil contacts for improved water uptake. As shown previously both *B. commutatus* and *B. mollis* show reduced germination at low water availabilities and these conditions are likely to occur more frequently on the stubble surface.

The ecological advantage of protracted germination within an arable ecosystem, subjected to numerous disturbances, is that a proportion of the seeds, by remaining ungerminated, survive through such events as herbicide applications and seed bed preparations (Bulmer, 1987). Remaining seeds are then potentially available to germinate once the crop is sown and the environment becomes temporarily more stable. *B. interruptus* by exhibiting rapid germination is more vulnerable to large seedling losses at this stage of the life cycle.

Early germination does have advantages with regards to competition, both intra and inter- specific. It has been reported that early germinating *B. sterilis* plants were competitively superior to later germinators (Bulmer, 1987).

In contradiction to the expectation that fewer seeds would be lost from the stubble, due to human error in the relocation of buried seed in the cultivated treatment, there was a greater loss from the stubble than the cultivated treatment. The differences in numbers of seeds unaccounted for between the two treatments can most easily be explained in terms of seedling mortalities being greater on the stubble surface. An alternative explanation is that of predation. The seeds on the surface would be more visible to small mammals foraging through the stubble but if this was the case one might expect some differences between species due to preferential predation. No species preference was indicated by the analysis despite the differences in seed size (Table 1.4.a) which might be expected to favour the predation of *B. sterilis,* having a larger seed.

2.6 The survival of seedlings under vehicle passage.

The aim of this experiment was to investigate the effect of vehicle passage on the survival of established grass seedlings.

2.6.1 Materials and Methods

In this experiment three brome species, namely *B. commutatus, B. interruptus* and *B. sterilis* plus winter wheat, cv Avalon, were investigated under four intensities of vehicle passage. Vehicle passage was applied by the use of an Iseki tractor, the number of passes varying between treatments. The treatments were either single passage, double passage or quadruple passage with a control of no vehicle passage. The Iseki tractor weighed 540 kg, had 0.2 m wide rubber tyres and at the time of the experiment the tread on the front tyres measured 7 mm and on the back tyres 13 mm.

The susceptibility to damage according to developmental stage was investigated by the inclusion of two growth stages. The first treatment was applied to plants at the 1 - 2 leaf stage, hereafter referred to as GS 1 and the second at the 3 - 4 tiller stage, hereafter referred to as GS 2. All treatment/species combinations were replicated three times for each growth stage.

The experiment was arranged as a split split plot randomised block design with plots 1.6 m x 1 m, this size being dictated by the dimensions of the tractor. Since the rear tyres were 0.2 m wide four adjacent passes ensured a single pass over all of the plot area. This necessitated large turning areas for the tractor so as each successive pass could be applied correctly.

Each of the three replicate blocks were divided into main plots of equal halves for the two growth stages. Main plots were then subdivided into four sub plots to which vehicle passage treatments were individually applied, the order being randomly arranged. Within each sub plot, sub sub plots of the four species were randomised. Individual plots were separated by 0.5 m wide paths, sub plot treatments by 1 m wide paths and main plots, growth stages, by 5 m to allow tractor access.

All four species were sown at a rate of 1000 seeds m^{-2} on 24.11.89. Vehicle passage treatments occurred on 22.2.90 and 27.3.90, the initial treatment being delayed until the 3 - 4 leaf stage due to water logging preventing earlier access to the field.

Counts of seedling numbers were taken immediately prior to vehicle passage and at two subsequent dates, 3 and 6 weeks after treatment. Counts in two quadrats, both 0.04 m^{-2}, per plot were used, their positions marked by small canes to facilitate relocation.

At maturity, measures of seed production for *B. interruptus* were obtained by harvesting and threshing all the plants within a randomly placed 1 m^2 quadrat from each plot.

2.6.2 Analysis

The percentage survivorship, numbers surviving at monitoring as a percentage of the number prior to treatment, was calculated for all species and treatments for both monitoring dates. The results were then analysed by a mixed model analysis of variance for a randomized block split split plot design to take into account non orthogonality due to unequal cell sizes (SAS, 1985). Unequal cell sizes occurred due to missing data for some replicates within sub-sub plots. These replicates were subsamples within the species plots and therefore nested under them. Blocks were considered a fixed effect following Winer (1971). Standard errors of the means were calculated, where appropriate, for comparison of the means.

Seed production for *B. interruptus*, measured as weight of seeds produced per unit area, was analysed by analysis of variance for a split split plot design (SAS, 1985).

2.6.3 Results

The winter wheat either failed to germinate or the seedlings were destroyed by a pest (probably geese) within the first two weeks after emergence as no crop seedlings had established by the beginning of January 1990.

The analysis of variance of survivorship for the three species at the first monitoring date, three weeks after the vehicle passage treatments (Table 2.6.a), showed a significant interaction between growth stage and species ($P < 0.02$). This interaction indicated that the survivorship of seedlings at the two growth stages differed amongst the three species. *B. commutatus* and *B. sterilis* showed greater seedling mortalities when the vehicle passage treatments were applied at the later growth stage of 3 - 4 tillers, GS 2, compared to the earlier growth stage of 3 - 4 leaves, GS 1. However, *B. interruptus* displayed increased mortalities at the early growth stage when compared to the later stage (Figure 2.6.1). Comparison of the means, with an SEM of 2.32, showed that only *B. commutatus* differed significantly between GS 1 and GS 2.

The analysis of variance of survivorship at the second monitoring, six weeks after the vehicle passage treatment (Table 2.6.b) showed that the growth stage at which the vehicle passage treatment occurred may have had an effect on the percentage survivorship of the seedlings. However, this effect was only significant at $P < 0.10$. Survival of the seedlings which received the vehicle passage treatment at GS 1 was reduced compared to that at the GS 2. The overall percentage survival at GS 1 was 73.82 % compared to 85.37 % at GS 2. There were no other significant effects or interactions.

The analysis of variance of the seed yields for *B. interruptus* under the vehicle passage treatments at both growth stages showed a significant interaction between growth stage and treatment ($P < 0.44$). As can be seen, Figure 2.6.2, this interaction occurred due to the substantial difference in yields between the controls at GS 1 and GS 2. The three replicates at GS1 produced consistently higher yields than those at GS2. The yields at GS 1 were 209.3, 168.8 and 103.1 g m^{-2} compared to yields of 87.7, 92.9 and 45.1 g m^{-2} at GS 2. None of the treatments produced significant differences in yield between GS 1 and GS 2. At GS 1 there was a trend of decreased seed production with increased vehicle passage but the differences in the treatment means were not significant, compared with an SEM of 17.35, nor was the trend apparent at GS 2.

Table 2.6.a Analysis of variance of the percentage survivorship for seedlings under three intensities of vehicle pressure at the first monitoring, three weeks after the vehicle passage treatment. Type III sums of squares used.

Source	d.f.	M.S.	F	$P_{(Ho)}$
Main Plots				
Blocks	2	367.38	3.60	NS
Growth Stage (GS)	1	160.69	1.57	NS
Main Plot Error	2	102.15		
Sub Plots				
Vehicular Passage (VP)	3	255.29	1.58	NS
GS x Species	3	225.22	1.40	NS
Sub Plot Error	12	161.01	161.01	
Sub-Sub Plots				
Species (S)	2	96.44	0.32	NS
Replicates within S	3	304.90		
S x GS	2	507.34	3.93	<0.05
S x VP	6	144.87	1.12	NS
S x GS x VP	6	234.73	1.82	NS
Sub-Sub Plot Error	88	128.99		
Total	130	148.58		

Table 2.6.b Analysis of variance of the percentage survivorship for seedlings under three intensities of vehicle pressure at the second monitoring, six weeks after the vehicle passage treatment. Type III sums of squares used.

Source	d.f.	M.S.	F	$P_{(Ho)}$
Main Plots				
Blocks	2	1.47	0.0082	NS
Growth Stage (GS)	1	3106.88	17.41	<0.10
Main Plot Error	2	178.45		
Sub Plots				
Vehicular Passage (VP)	3	106.45	0.55	NS
GS x Species	3	163.71	0.72	NS
Sub Plot Error	12	194.62		
Sub-Sub Plots				
Species (S)	2	100.17	0.62	NS
Replicates within S	3	156.18	0.496	NS
S x GS	2	700.69	2.23	NS
S x VP	6	459.13	1.46	NS
S x GS x VP	6	357.92	1.14	NS
Sub-Sub Plot Error	78	314.80		
Total	120	328.37		

Table 2.6.c Analysis of variance of the seed yields for *B. interruptus* at two growth stages, under three intensities of vehicle passage with a control of no passage. Type III sums of squares used.

Source	d.f.	M.S.	F	$P_{(Ho)}$
Main Plot				
Block	2	7307.24	8.09	0.0060
Growth Stage (GS)	1	1612.78	1.79	0.2062
Main Plot Error	2	1873.33		
Sub Plot				
Vehicle Passage (VP)	3	621.57	0.69	0.5763
GS x VP	3	3318.16	3.68	0.0436
Sub Plot Error	12	902.84		
Total	23	1853.36		

Figure 2.6.1 Mean seedling survivorship, over all treatments, for the three brome species at the two growth stages, at the first monitoring.

SEM = 2.32

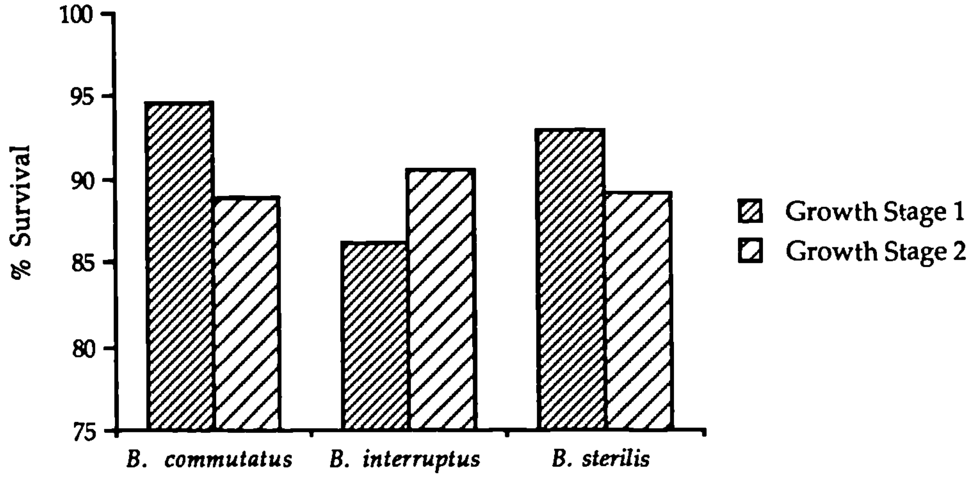
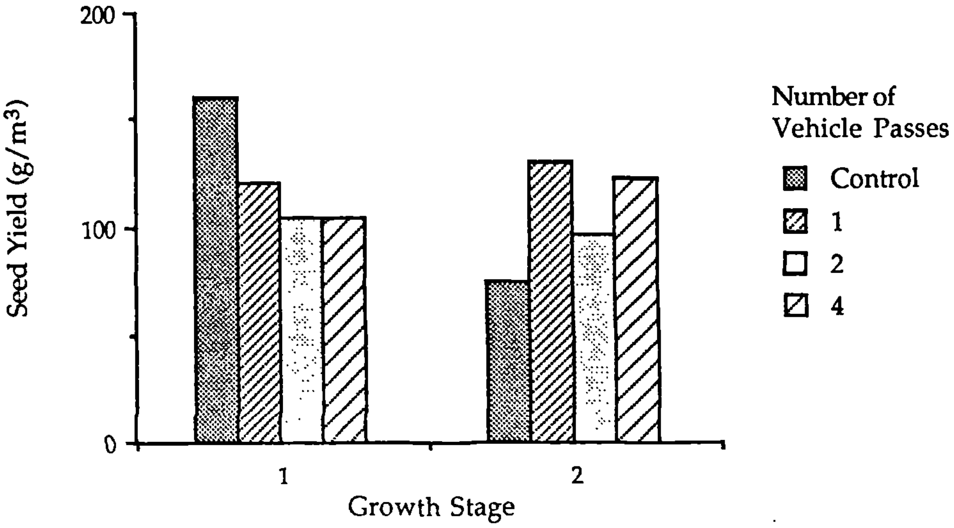


Figure 2.6.2 Seed yield of *B. interruptus* after recieving differing intensities of vehicle pressure applied at two growth stages.

SEM = 17.35



There was a significant difference in yields between the three blocks, the third block had a reduced yield of 80.7 gm^{-2} compared to the other two blocks which had yields of 126.0 and 138.0 gm^{-2}.

2.6.4 Discussion

The results presented here showed that under the conditions of this experiment all three brome grasses used in this study were tolerant of low intensity vehicle pressure as none of the vehicle passage treatments produced a significant reduction in seedling survivorship. However, some differences in response were detected during the experiment.

At the first monitoring, three weeks after treatment, there was a significant interaction between the growth stage at which the treatment was applied and the species due to *B. commutatus* showing a significant difference in survivorship between GS 1 and GS 2 that was not shown by the other two species. *B. interruptus,* in contrast with *B. commutatus* and *B. sterilis,* suffered greater mortality at the first rather than second growth stage. This difference amongst species was no longer apparent at the second monitoring, six weeks after treatment. At the second monitoring all three species showed reduced survival when the vehicle passage was applied at GS 1 compared to GS 2. This indicated that *B. interruptus* GS 1 seedlings responded to vehicle passage treatment faster than the other two species.

The lowered survivorship recorded for the plants, which experienced vehicle passage treatments at GS 1 indicated that the developmental stage at which vehicle pressure was experienced influenced the extent of seedling mortality. The further advanced plants, GS 2, survived in greater numbers. This difference may be due to the plants that had tillered before treatment having a greater chance of survival. If the meristem was damaged no further growth would be possible. Tillered plants, having a greater number of meristems were less likely to suffer mortality of the whole plant than the plants with only a single meristem. Even if one or two tillers were destroyed as a result of vehicle passage the plant as a whole may survive through the growth of the other remaining tillers. Related work in the literature does not unambiguously support this argument. Ellis (1981) defined the verdure of a grass sward as the dry weight of grass material per unit area and used measures of the verdure to compare the wear tolerance, and hence survivorship, of eight cultivars of *Lolium perenne* L. He reported that verdure and turf density after the treatment of 850 pedestrian passes directly correlated with verdure and turf density prior to treatment. The wear tolerance of each sward appeared to be directly related to the quantity of material present in the sward before treatment. However, Shearman and Beard (1975a; 1975b; 1975c) reported that differences in wear tolerance amongst seven grass species were related to cell wall constituents and not verdure, shoot density, leaf tensile strength, or relative turgidity.

The seed yields for *B. interruptus* under vehicle passage treatments provided further evidence for the ability of these species to tolerate light vehicle pressure. The only significant difference in the mean yields at the two growth stages was between the two controls. As controls neither had received any form of vehicle passage or any other differences in management regime, no explanation for this difference can be given other than experimental variation.

At GS 1 there was a trend of decreased yield with increased vehicle passage, although the mean yields did not differ significantly. This trend was not apparent at GS 2. These results again indicate that GS 1 was more sensitive to vehicle pressure than GS 2, although due to the lack of significance of these differences between growth stages this difference in sensitivity could only be slight.

The third block of the experimental design consistently produced lower seed yields than the other two blocks. This was due to a weed infestation throughout the block.

One criticism of any field experiment such as the one reported here is that the results only apply to the specific conditions in which the experiment was conducted and therefore care must be taken when making generalisations based on these results. The factors that would influence the effects of vehicle pressure in such an experiment are numerous and some would be beyond the control of the experimenter. For example, soil compaction due to vehicle passage has been shown to be more severe when soil moisture content was high (Douglas & Campbell, 1987; Douglas & Crawford, 1988).

However, there are several factors the effects of which could easily be investigated. Intuitively the growth stage of the plants at the time of the vehicle passage is thought to be influential on their ability to tolerate, or recover from, the treatment. Latter developmental stages than studied in this experiment may suffer greater damage, for example, once the inflorescence was erect damage may be irreparable. Further studies should cover a wider range of plant developmental stages. Differences in the shear forces exerted during the treatment could be investigated via alteration of the tyre tread depth and tractor weight. The influence of these factors would also depend crucially on soil moisture content. In the experiment reported here, shallow tread tyres were used which would produce smaller tearing forces than larger tread tyres especially on wet soils. Due to the lack of any significant treatment effects detected here a greater range of vehicle pressure treatments could usefully be investigated to determine the vehicle pressure at which damage becomes appreciable.

Various authors have studied the effects of human and animal trampling on plant communities (Thomas, 1960; Streeter, 1970; Harrison, 1981) but, until recently, few have looked at the damage caused by vehicle passage (Bates, 1935, 1937; Liddle, 1973). In the last decade, work has been conducted on the response of soil and crop performance to different levels of compaction by farm machinery (Chamen *et al.*, 1986; Douglas & Campbell, 1987; Douglas & Crawford, 1988). A decrease in species diversity with increased animal or human trampling was recorded by some authors (Bayfield, 1973; Liddle & Greig-Smith, 1975) whilst others reported the reverse (Westhoff, 1967; van der Maarl, 1971). This apparent dicotomy in results was explained by Liddle (1975) with reference to a hypothetical undisturbed, productive grassland. Low levels of trampling were sufficient to have a detrimental effect on the dominant species thus allowing other species to appear within the community, whilst high levels of trampling reduced the species diversity to only those resistant to this increased pressure. However, other authors (Streeter, 1971; Chapel *et al.*, 1971) have related increased numbers of species at low tramplings to higher concentrations of phosphorus in the soil of trampled zones. Work on the recovery of lowland grass swards after trampling (Harrison, 1981) showed that recovery related to the species growth rates. Different species were also noted for displaying different tolerances to the trampling pressure, for example, *Dactylis glomerata* showed resilience. In some situations the recovery was aided by the increased nutrient cycling that resulted from the dead plant material being incorporated into the soil. This effect was most noticeable on the swards that contained species that respond vigorously to fertilizer additions.

The results reported here contrast with those discussed above for the effects of human and animal trampling where substantial damage to the vegetation was recorded. One explanation for the limited effects reported here compared to the work on animal and human trampling is the difference in severity of the treatments. All the work on human passage looked at high intensities of trampling, often dealing with several hundred or even thousand passes. Also the shear forces involved during the action of walking are greater than those involved during vehicle passage (Liddle, 1975).

Work on the effects of three intensities of tractor wheel pressure on the performance of a grass sward grown for silage over several years (Douglas & Campbell, 1987; Douglas & Crawford, 1988) initially showed no overall treatment differences in the first year. However, significant reductions were apparent the following year in both the growth rates of the constituent grass species and the biomass yields at harvest. The authors suggested the reductions were possibly due to the effects of both physical damage to the plants due to the wheelings as well as impaired nitrogen uptake from the compacted soil. In both years a compaction of the top soil was evident from the increased readings for soil bulk density and shear strength but the extent of the compaction was dependant on the water status of the soil, compaction being more severe for wet soils.

These results indicate that the effects of compaction of the top soil on grass swards are cumulative over time assuming no cultivation. If exposed to repeated compactions the bromes may also show yield reductions. However, if established in a headland area subjected to annual cultivations the cumulative compaction effects may not occur and therefore yields may be unaffected. The implication of the results is that the brome species will tolerate light vehicle pressure once the plants are established with no detectable effect on plant mortalities or seed production. This conclusion is supported by the report that *B. mollis* is known to be tolerant of animal trampling existing as a dominant grass in some drought prone, trampled areas (Grime, 1979). If these species are tolerant of low intensity vehicle pressure, as these results suggest, then they will be able to exploit headland areas as potential habitat sites.

2.7 Influence of planting date on flowering.

The aim of this experiment was to investigate the influence of successively delayed planting dates on the flowering and subsequent seed production of the four bromes.

2.7.1 Materials and Methods

Seed of the four brome species were sown at monthly intervals over a period of four months, from February to May 1988, into 25 cm diameter pots, containing John Innes No 5 compost. 30 seeds were sown and upon germinating the seedlings were thinned by hand to leave 10 plants per pot. Three replicate pots were sown for each species at each sowing date. Seed stock, harvested the previous autumn, had been stored in a dark, unheated room.

Pots were arranged in three randomised blocks of sixteen and placed outside under field conditions. Sowing of the seeds took place in situ on 11.2.88, 11.3.88, 11.4.88 and 11.5.88.

Plants were monitored on 23.8.88 and scored according to presence/absence of seeds and seed maturity where present. Maturity was considered as the formation of hardened caryopses.

2.7.2 Results

The four species showed noticeable differences in their responses to planting date. All four species produced seed from the earliest planting in February but in *B. mollis* seeds were immature at the time of harvest in August. In all plantings after 11.2.88 *B. mollis* failed to set seed. The other three species produced seed from the material planted in March but for *B. sterilis* one of the three blocks failed. However, only seed of *B. sterilis* had ripened by the time the experiment was scored. *B. commutatus* and *B. interruptus* alone produced seed in the April planting, with *B. commutatus* only setting seed in two of the three blocks. Neither species displayed ripened seed at harvest (Table 2.7.a).

None of the four species set seed in the latest planting date of May.

Table 2.7.a Influence of sowing date on the seed production of the four brome grasses when planted in the spring. Plants scored according to the presence / absence of seed and if present whether mature on 23.8.88.

R - seed present and ripe

G - seed present but immature

* - no seed produced.

Species		Seed Production Time of Planting (Month)			
	Block	February	March	April	May
B. commutatus	1	R	G	G	*
	2	R	G	*	*
	3	R	G	G	*
B. interruptus	1	R	G	G	*
	2	R	G	G	*
	3	R	G	G	*
B. mollis	1	G	*	*	*
	2	G	*	*	*
	3	G	*	*	*
B. sterilis	1	R	R	*	*
	2	R	*	*	*
	3	R	R	*	*

Table 2.7.b Monthly temperatures, at grass level, during the experimental period from February to May 1988. Data from weather station DCNN 7326, Ness Gardens.

	Air Temperature (°C)		
Month	**Mean**	**Max.**	**Min.**
February	2.2	5.7	-0.6
March	3.5	6.8	-1.5
April	4.7	10.9	-1.8
May	7.2	10.0	3.3
June	10.7	13.6	6.6
July	11.4	14.4	7.8

Table 2.7.c The number of days below 2 °C and between 2-5 °C for the month following each planting date over the period February to May 1988. Data from weather station DCNN 7326, Ness Gardens.

In the month following planting of seeds on:	**Number of days:** below 2 °C	between 2-5 °C
11.2.88	13	13
11.3.88	3	20
11.4.88	4	7
11.5.88	0	2

2.7.3 Discussion

The time of first flowering of *B. sterilis* has been shown to recede with increasing delay in the planting date. Froud-Williams (1983) reported that the flowering of plants sown between August - January occurred in May - June, plants from February sowings flowered in June - July and March - April sown plants flowered between late July - September. The plants at these very latest planting dates showed a reduction in the size and number of seeds produced. Similar results had previously been reported by Budd (1981) who recorded that 50 % of *B. sterilis* seeds had shed by mid August from plants sown in late February. Gray (1981) reported that *B. sterilis* plants which emerged in April flowered between July and September of the same year. The results reported here show *B. sterilis* plants having flowered and set seed only for the two earliest planting dates of February and March.

There are two main mechanisms for the initiation of flowering in plants, either via vernalisation or photoperiodism (Wareing & Phillips, 1981). Vernalisation involves exposure of the plant to temperatures between -1 to 9 °C, 1 - 4 °C being the most effective temperature range, for a period of time. The length of time required to initiate flowering varies between species and within a species prolonged exposure to cold temperatures can hasten flowering (Wareing & Phillips, 1981). Photoperiodism is the initiation of flowering by certain daylength exposures, these requirements are species specific. The mechanism is controlled by the ratio of the two forms of phytochrome, P_{fr} and P_r, within plant leaves. Photoperiodic responses can be of two main forms; initiation of flowering by exposure to short daylengths or long daylengths. Requirement of combinations of short and long daylength exposures are also possible (Wareing & Phillips, 1981).

Laboratory experiments have indicated that a vernalisation period at 4°C promoted the flowering of *B. sterilis* but was not essential (Froud-Williams, 1983).

Work on *B. commutatus* (Finnerty & Klingman, 1962) showed a requirement for a vernalisation period or a period of exposure to short days prior to long days was necessary for flowering to occur. Hulbert (1955) reported that the numbers of spikelets for spring germinated plants in nine out of the ten brome species studied, which included

B. commutatus, were reduced. Only *B. rubens* L. produced comparable numbers of spikelets regardless of planting date.

The results reported here indicate that the four species display a range of requirements for the "trigger" that initiates flowering. *B. mollis* only produced seed at the earliest planting date indicating that some vernalisation period or photoperiod experience is necessary. The temperatures recorded over the period of the experiment (Table 2.7.b) do show a substantial decrease in the number of days below 5 °C, in the month following planting, with each successive planting date. If a vernalisation period is required then the indication is that *B. mollis* requires lower temperatures, or a longer period at low temperature, for vernalisation than the other three species.

The plants of *B. commutatus* and *B. interruptus* from the April sown material flowered which indicated two possibilities. Either, if vernalisation initiated flowering then *B. commutatus* and *B. interruptus* responded to a shorter cold period than *B. mollis* or if photoperiodism controlled flowering then *B. commutatus* and *B. interruptus* were sensitive to smaller changes in photoperiod than *B. mollis*.

Further work would be necessary to establish if these four species responded to vernalisation, photoperiodism or a combination of the two. Investigations of photoperiod effects at constant temperature and conversely, cold exposures at constant photoperiods would be necessary to isolate which mechanism was initiating flowering in these four grasses.

Gray (1981) suggested that the development of the inflorescence is controlled by an environmental factor, most probably the photoperiod experienced by the plant, and that the ecological advantage of this is a closer synchronisation of flowering within a population. Although all these species are known to be self fertile (autogamous) it is thought that, for grasses, cross fertilization increases fertility (Beddows, 1931).

2.8 The rate of seed dissemination

The experiment reported here was designed to obtain data on the rates of seed dissemination of the four brome species.

2.8.1 Materials and Methods

Individual plants of all four brome species were raised in the field and destructively harvested during the course of the summer. The experiment followed a split plot design with sub plots of each of the four brome species being grown in the field, with main plots being either the presence or absence of a winter wheat crop. This design incorporated sub plots enabling 20 destructive harvests, each of 10 replicate plants of each of the four species.

Each plant was grown at approximately the centre of a 0.25 m^2 plot. The ten replicates were arranged as separate blocks, each block divided into quarters by 0.5 m wide paths to allow access. Blocks were separated by 1 m paths. The position of the plots representing each harvest/species combination was completely randomised within each block.

The winter wheat cv Avalon, was sown at 138 kg ha^{-1}, on 12.10.88. At the time of sowing 20 kg N ha^{-1}, in the form of Nitram, was incorporated into the seed bed. A further dressing of fertilizer was applied on 21.2.89 at a rate of 70 kg N ha^{-1} again as Nitram to the wheat plots only.

Harvesting commenced at the time the first species achieved maturity. Harvests occurred at weekly intervals from 30.6.89 until 2.11.89 at which point it was no longer feasible to find the remaining plants due to lodging of the crop and developing weed flora around the spaced plants.

2.8.2 Analysis

Initially the number of seeds remaining per plant was analysed by analysis of variance for a split plot design (SAS, 1985). Data were then meaned over all replicates, log transformed and analysed by linear regression. The regression coefficients calculated in this analysis are equivalent to a measure of the rate of seed loss per plant, in terms of the number of seed retained, hence being negative values (Table 2.8.b).

2.8.3 Results

Analysis of variance for the sixteen harvests showed that there was a significant ($P<0.0001$) decline in the number of seeds per plant over time. The mean of seed numbers per plant, over all species under both treatments, at the first harvest was 642.3. This had declined to 156.9 by the sixteenth harvest. The treatment of plants grown either as spaced plants or in a wheat crop also had a significant effect on the number of seeds per plant ($P<0.0001$). The average, over all harvests and species, for spaced plants was 858.8 compared to 88.3 for plants grown in the crop, an approximately ten fold difference.

The grasses also showed differences in the mean number of seeds they produced ($P<0.0001$) and there was a significant interaction between the species and the treatments ($P<0.0001$). This indicated that the four species responded differently to the treatments. Seed production in *B. commutatus* and *B. mollis,* when grown as spaced plants was roughly twice that of *B. interruptus* and *B. sterilis*. Mean seed numbers were 1357.7 and 1032.0 for *B. commutatus* and *B. mollis* compared to 512.9 and 546.6 for *B. interruptus* and *B. sterilis,* respectively. The interaction between the time of harvest and the treatments was statistically significant ($P<0.0001$) which indicated that the difference in numbers of seeds remaining per plant between the two treatments was not constant over time(Table 2.8.a).

A significant difference was detected amongst replicates ($P<0.0001$), these differences were due to the variability inherent in using single plants as replicates especially when grown in a field situation which is in itself variable. Monitoring consisted of destructive harvests of ten replicate plants of each species, at each harvest. Greater replication would be expected to reduce the variation apparent in Figure 2.8.1 and Figure 2.8.2.

Figure 2.8.1 shows the marked decline in the mean number of seeds remaining per plant, for the ten replicates of each species, under both treatments. The differences in mean number of seeds per plant at peak maturity between the plants grown in monoculture and those raised in the crop are apparent. The effect of the treatment on the rate of seed loss, shown by the regression lines, is also marked, the change in rank order of the species between the two graphs being obvious.

From the regression coefficients (Table 2.8.b) it can be seen that the presence of the wheat crop had no significant effect on the loss rate of either *B. interruptus* or *B. sterilis*. However, the effect of crop presence on the regression coefficients for *B. commutatus* and *B. mollis* emphasise the marked difference in the loss rates between the two treatments apparent in Figure 2.8.1.

The three way interaction amongst harvest time, treatment and species was significant ($P<0.0145$). This interaction is best explained with reference to Figure 2.8.1 which shows the rates of seed loss for the four species under both treatments. These graphs show that although rate of loss was constant for each species it was different amongst the species and between the treatments. For example, *B. commutatus* had the lowest rate of loss when grown as spaced plants but the second greatest when plants were grown in wheat.

The regression coefficients calculated on the mean of the ten replicates for each species/treatment/harvest combination (Table 2.8.b) indicate the loss rates for plants grown in wheat ranked as follows;

B. mollis > *B. commutatus* > *B. sterilis* > *B. interruptus* whereas for the spaced plants in monocultures the loss rates ranked;

B. sterilis > *B. interruptus* > *B. mollis* > *B. commutatus*

Although previous field observations (section 3.2) had indicated that *B. sterilis* shed all its seed very rapidly, within a month of ripening, the data showed that *B. sterilis* disseminated seed over much longer periods for both spaced plants and those grown in wheat. The graphs of number of seeds remaining as a percentage of the maximum at peak maturity, Figure 2.8.2, show that *B. sterilis* displayed a rapid decline in the number of seeds retained over the first month but that approximately 50 % still remained on the plants at the end of this period. These seeds were disseminated over the following 100 days, with a similar small fraction still remaining on the plants regardless of the presence

Table 2.8.a Analysis of variance of the numbers of seeds remaining per plant, for all replicates of all four species, over 16 harvests. Both the treatments of plants grown 1) in spaced conditions in monoculture or 2) on a similar spacing pattern but in a winter wheat crop, were included in the analysis. Type III sums of squares used.

Source	d.f.	M.S.	F	P(Ho)
Main Plots				
Treatment (Tmt)	1	183464007.38	45.50	0.0001
Main plot error	9	4032010.40		
Sub Plots				
Harvest (Harv)	15	3652330.41	15.32	0.0001
Species (Spp)	3	10856777.28	45.53	0.0001
Replicate (Rep)	9	4350970.06	18.25	0.0001
Harv x Spp	45	321695.89	1.35	0.0641
Tmt x Spp	3	15350254.11	464.38	0.0001
Harv x Tmt x Spp	45	365475.27	1.53	0.0145
Sub plot error	1062	238438.03		
Total	1207	587723.12		

Table 2.8.b Regression coefficients (equivalent to loss rates), for mean number of seeds per plant (log transformed) recorded for the four species over the 1989 summer, under the two treatments of plants grown either as spaced plants in monocultures or in a cereal crop.

	Treatment			
Species	Spaced plants		Within crop	
	Regression Coefficient	Standard Error	Regression Coefficient	Standard Error
B. commutatus	-0.00443	0.000540	-0.01052	0.000906
B. interruptus	-0.00667	0.000987	-0.00752	0.001050
B. mollis	-0.00623	0.000789	-0.01180	0.000727
B. sterilis	-0.00963	0.000786	-0.00951	0.000781

Figure 2.8.1 Rate of seed loss for the four brome grasses under two treatments a) grown as spaced plants in monoculture and b) grown under the same spatial arrangement as a) but in the presence of a winter wheat crop. Data values plotted were the mean number of seeds remaining per plant for ten replicate plants. Regression analysis of fitted lines is given in Table 2.8.b.

Note log scale on vertical axis.

Note ordinates are scaled differently.

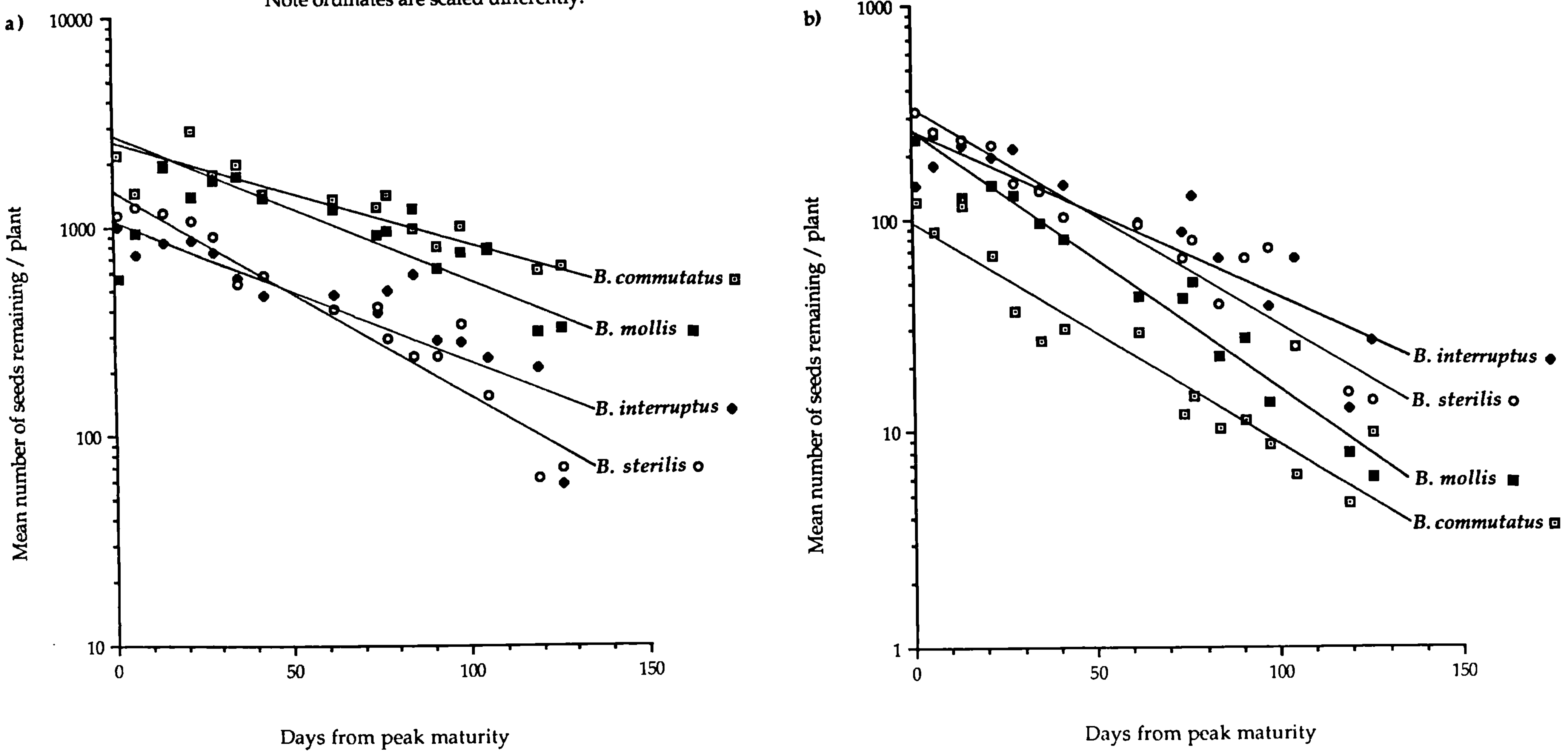
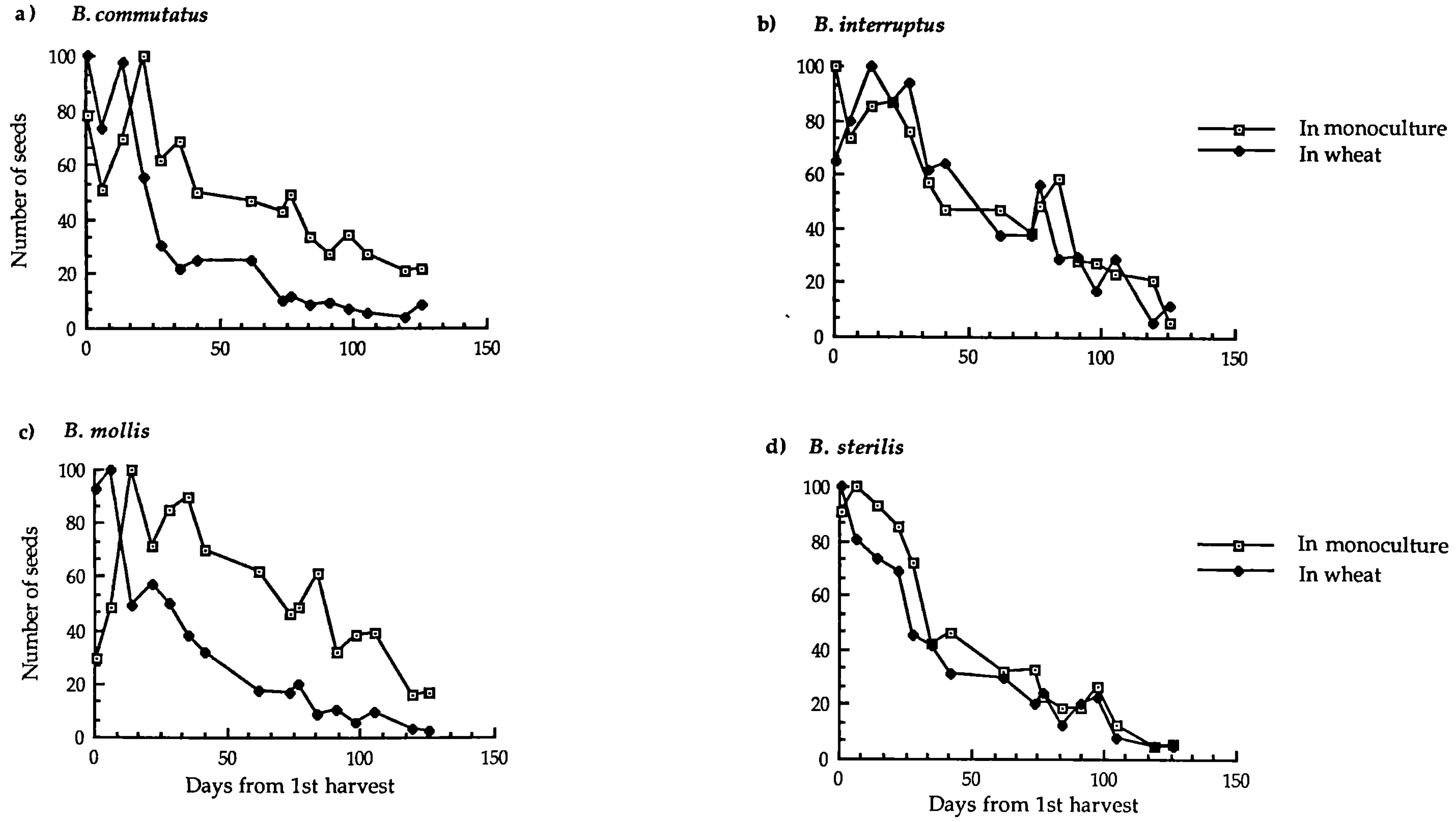


Figure 2.8.2 Mean number of seeds remaining per plant, as a percentage of the maximum at peak maturity, for the four brome grasses under two treatments, plants in monoculture and plants grown in wheat. Data values represent the mean of ten replicate plants.



of wheat. Like the *B. sterilis, B. interruptus* showed a very similar rate of loss under both treatments but at a slower rate, 50 % loss occurring after approximately 50 days.

B. commutatus and *B. mollis* both showed later maturity compared with *B. sterilis* and this difference was more obvious in the spaced plants. Both species also displayed a marked difference in the rates of loss between the two treatments, mainly (Figure 2.8.2) due to a very rapid decline in seed numbers over the first twenty days from when maturity was reached in the wheat.

2.8.4 Discussion

The results reported here showed that the presence of the crop influenced the speed at which the seed of the brome species matured, however there were also inherent differences between the species. *B. commutatus* and *B. mollis* appeared to mature later, by 7 -10 days, than *B. sterilis* both in the spaced conditions and when grown in the presence of wheat. With the exception of *B. interruptus* the species matured earlier when grown in the presence of the crop (Figure 2.8.2). Work on the dissemination of *Avena fatua* (Wilson,1981) in winter and spring cereals showed that the crop within which the weeds were growing influenced the timing of maturity of the weed. The wild oats matured sooner in the earlier maturing winter cereals. The time at which maturity is reached is important as all four brome grasses started to disarticulate their seed once ripe, following the third pattern of slow release discussed in section 2.1. The time at which plants mature and also their rates of dissemination are influenced by the weather, dry conditions hastening both characteristics (Wilson, 1970).

Differences in loss rate amongst the species can be, in part, explained by differences in panicle morphology. *B. interruptus* had a very compact panicle with short branches (Plate 1) and consequently spikelets existed in clusters over a panicle length of upto 70 mm. The panicles of *B. commutatus* and *B. mollis* were similar in shape, usually longer than *B. interruptus*, and with longer branches. *B. sterilis* panicles were loose and longer than those of *B. commutatus* and *B. mollis* . The results reported here indicated that other factors were also involved in the control of loss rates besides panicle morphology as the loss rates of B. *interruptus* and *B. sterilis* were similar under both treatments where as *B. commutatus* and *B. mollis* showed a substantial increase in dissemination rate when grown in the presence of a wheat crop. Why two of the four species showed this effect was unclear.

2.8.4.1 The ecological significance of differences in rate of seed loss.

The ecological significance of variations in dissemination rate relates to the fact that the numbers of seed remaining on the plants at the time of crop harvest differ between the four species. These differences affect the relative importance of crop harvest on the dispersal of the grasses. As shown by Wilson (1970) and a subsequent experiment reported in this thesis (section 4.3) there is a substantial amount of weed seed that passes through the combine at harvest, returning to the seed bed with the straw and chaff. The actual numbers and the proportion of the total weed seed this will be depends directly on the amount of seed on the plants at harvest. Of the seed entering the combine harvester not all is returned to the soil surface. A substantial percentage enters the storage tanks along with the cereal grain and is thus lost to the field population. Seed shed prior to harvest will remain in the area surrounding the source plant whereas that entering the combine harvester can potentially be displaced over greater distances. Looking at the data for the four bromes grown in wheat (Figure 2.8.2) it can be seen that differences occur between species in the percentage seeds remaining on the plant and therefore available for harvest at the end of August, the normal harvest time. Both *B. commutatus* and *B. mollis* have fewer seeds remaining, approximately 20 % and 25 % respectively, compared to the *B. interruptus* and *B. sterilis* which have 45 % and 35 % respectively. Taking into account the comparatively greater seed production of the latter two species in wheat it becomes obvious that populations of *B. interruptus* and *B. sterilis* will be more susceptible to losses at harvest and also experience greater dispersal of seeds during the harvesting process.

However, prolonged dissemination can have ecological advantages especially for *B. interruptus* which has previously been shown to display the potential for rapid germination once in contact with the soil. The prolonging of dissemination is a form of temporal dispersal and increases the chance of seed germinating and establishing within the temporally heterogeneous environment of an arable ecosystem.

The following table, Table 2.9, summarises the results and implications of the autecological experiments reported in this chapter.

Table 2.9 Autecological summary of the results from the experiments reported in this chapter.

Experiment		**Species**			
		B. commutatus	***B. interruptus***	***B. mollis***	***B. sterilis***
Germination					
1) over temperature range	Fastest germination at:	20 °C	25 °C	20 °C	20/25 °C
	Reduced nos. after 14 days at:	25 °C	*	*	*
Conclusion:	With the exception of *B. interruptus* germination rate increased with temperature upto 20 °C.				
2) over water availability range	Reduced nos. after 27 days at:	Med Occ Low Occ	*	Med Occ Low Occ	Med Freq Low Occ
		(see Table 2.3.a for explanation of codes)			
Conclusion:	With the exception of *B. interruptus*, which showed similar rates throughout, germination rate increased with water availability.				
3) on stubble surface	Significant reduction in rate on stubble	Yes	No	Yes	Yes
Conclusion:	Species germinated faster when covered with a 5 mm layer of soil compared to when sown on the stubble surface.				
Establishment from depth	% established from:				
	10 mm	92	100	98	97
	50 mm	60	8	15	5
	100 mm	4	0	5	2
Conclusion:	All species showed limited establishment from depth with differences apparent amongst the species at a planting depth of 50 mm.				
Vehicle pressure	All species appeared to be tolerant of light vehicle pressure.				
Photoperiod Vernalistion requirement	Date of latest planting for seed production	April	April	February	March
Conclusion:	All four species have some photoperiod/vernalistion requirement to initiate flowering but variation in this requirement exists amongst the species.				
Dissemination rate			Loss rate (x 10^{-3})	time^{-1}	
	Spaced plants	-4.43	-6.67	-6.23	-9.63
	Plants grown in wheat	-10.52	-7.52	-11.80	-9.51
Conclusion:	*B. interruptus* and *B. sterilis* displayed similar loss rates both as spacedplants and when grown with wheat. *B. commutatus* and *B. mollis* showed an increase in loss rate when grown in wheat compared with spaced plants.				

Chapter 3

Population Ecology

3. Population ecology

3.1 Introduction

3.1.1 Studies of the population ecology of annual plants.

Watkinson (1981a) commented that an understanding of population numbers, in demographic terms, requires a knowledge of how fecundity and survivorship vary with density. He went on to say that this knowledge is best achieved by monitoring populations at densities both above and below those that are naturally observed. Until the last decade the majority of studies of the population ecology of annual plants were based on agricultural systems (Watkinson, 1981a), investigating the population dynamics of weeds. The simplicity and diversity, as well as the potential for experimental modification, of agricultural ecosystems are advantages in such studies (Snaydon, 1980). The recent trend of modelling the population dynamics of weeds (Watkinson, 1981b) and their effects on crop yield (Firbank & Watkinson, 1986) has also lead to a greater understanding of the mechanisms of population regulation.

The application of this knowledge to the management of weed infestations has been discussed (Mortimer, 1987) emphasising the use of population ecology for the prediction of the behaviour of weed infestations (e.g. Zanin & Sattin, 1988) and control practices. Management strategies that have been studied include the effects of straw burning on *Avena fatua* (Wilson & Cussans, 1975), tillage and straw disposal on *Alopercus myosuroides* (Moss, 1987) and herbicides (Manlove, 1985; Ulf-Hansen, 1989). Recently the economics of such control strategies have also been included into the models of these systems (Doyle *et al.*, 1986; Cousens *et al.*, 1986).

Manipulative population dynamics studies of non agricultural annuals include the work on the sand dune annuals *Cakile edentula* (Keddy, 1981) and *Vulpia fasiculata* (Watkinson & Harper, 1978), as reviewed by Watkinson and Davy (1985) where the densities of naturally occurring populations were altered by addition of seeds or the thinning of seedlings. The effects of such manipulations on the subsequent reproduction of the plants was recorded with marked negative density dependence between seed production and plant density being noted.

The experimental techniques used in such studies have involved the use of either naturally occurring populations (e.g. Keddy, 1981; Wilson & Cussans, 1975), populations sown in to field conditions (e.g. Firbank & Watkinson, 1986; Zanin & Sattin, 1988) or pot experiments (e.g. Watkinson, 1981b). Pot experiments have the advantage of greater control over experimental conditions and the homogeneity of these conditions whereas field experimentation allows for larger plot size (and often larger experiments!). By sowing populations of seeds into soils otherwise devoid of that species an accurately known range of initial densities can be achieved and the resultant population sizes monitored over time. The use of field trials facilitates the achievement of very low densities, e.g. 1 seed m^{-2} and below, that would rarely be possible in pot experiments.

3.1.2 Competition.

The history and diversity of competition studies has been reviewed recently (Law & Watkinson, 1989) where competition was considered in relation to the evolution and population dynamics of competing species. Here only the latter is considered. A definition of competition was proposed by (Grime, 1973) in an attempt to distinguish this factor of plant interactions from the numerous other influences, both biotic and abiotic, that control plant population numbers and distribution. Competition was defined as "the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space". This definition stresses the mechanisms of competition rather than the effects (Grime, 1979).

Both prior to and since this clarification of the meaning of competition numerous studies have been conducted to investigate the effects of competition between and within species. Two main designs of experiment have been used widely, the additive and the substitutive designs. In the additive design one species is maintained at a constant density with varying densities of the second species in mixture with it, hence proving a popular design for studies of the competitive influences of weed infestations on crops (Donald, 1958; Welbank, 1963; Dew 1972; Young, 1988). Alternatively the substitutive designs maintain a constant overall density whilst varying the relative proportions of each species within the mixture. The formulation of a model to support this design (de Wit, 1960) further increased the popularity of this method and its wide spread use (de Wit & van den Bergh, 1965; Martin & Field, 1987; Fleming *et al.*, 1988).

3.1.3 Design of competition experiments.

In the last two decades several authors have expressed doubts about the use of both substitutive and additive experiments for the analysis of competition for either animal or plant populations (Connolly & Nolan, 1976; Inouye & Schaffer, 1981; Joliffe *et al.*, 1984; Firbank & Watkinson, 1985). Each design has associated disadvantages. With additive designs there is no separation between the effects of overall plant density and frequency of the individual species. However, with substitutive designs the effects detected can vary with changes in the overall density. This can only be determined by the development of the substitutive design to an addition series where the standard replacement series is repeated over a range of overall densities (Marshall & Jain, 1969; Pemadasa & Lovell, 1974). However, the effects of intra and inter specific competition still remain indistinguishable (Firbank & Watkinson, 1985). The use of replacement series experiments and the calculation of competitive indices from these experiments has recently been defended by Taylor and Aarssen (1989) with the limitation of using densities at which both species in monoculture would have achieved final constant yield. Few experimenters have looked at the effects of varying the densities of both species and their relative proportions, a situation more realistic for naturally occurring communities (Marshall & Jain, 1969; Wright,1981; Antonovics & Fowler, 1985; Firbank & Watkinson, 1985; 1986; Law & Watkinson, 1987; Sutton, 1988). The experiment reported here followed this design, the densities of both species were varied in all possible pairwise combinations.

3.1.4 Mathematical models of populations.

In arable ecosystems all four brome species behave as winter annuals, germinating in the autumn, flowering and producing seed in the summer. As already shown (Chapter 2) the majority of the seeds of all four species germinate during the late summer and early autumn resulting in approximately even aged populations without overlapping generations, assuming all the species have no persistent seed bank as shown for *B. sterilis* (Anon, 1981). The population dynamics of these species are therefore relatively simple to model mathematically. Plants with more complex life cycles, for example, *Senecio jacobeae* L., which show developmental stage differences within a population require more sophisticated models which take into account the possible stage transitions.

The mathematical models used to describe the population dynamics of species fall into two categories which reflect the basic difference in the life cycles of the populations they attempt to describe. Plants with overlapping generations are best described by differential equations. In contrast, plants with discrete generations, such as annuals, can be subject to census at one point in the life cycle and be modelled by difference equations. As the species in these studies are all annuals, with no persistent seed bank, they clearly fall into the second category.

The history of the mathematical modelling of populations has been reviewed by Watkinson (1980) as summarised below. A mathematical model for plant populations was proposed by Shinozaki and Kira (1956) who described the mean total dry weight production per plant by the following equation:

$$w^{-1} = A + B\ N$$

where A and B are constants, w is the yield per plant and N the plant density. This relationship, however, only describes an asymptotic yield - density relationship. Application of this basic model to a broader range of population data was achieved by the following modification of the equation (Bleasdale & Nelder, 1960):

$$w^{-\theta} = A + B\ N^{\phi}$$

where θ and ϕ are also constants. The ratio of these two constants determined the form of the yield - density relationship rather than their absolute values. Therefore Bleasdale (1966, 1967) concluded that it was acceptable to take ϕ as unity so the equation became:

$$w = (A + B\ N)^{-1/\theta}$$

This equation has since been reparameterised by Watkinson (1980) to the following:

$$w = w_m (1 + a N)^{-b} \qquad \text{(equation 1)}$$

where the following substitutions have occurred; b for q^{-1}, a for A^{-B} and w_m for $A^{-1/\theta}$.

The parameters in this equation now represent the following;

w_m - dry matter production of an isolated plant,

a - the approximate area required for production of a plant of weight w_m,

b - relates to the efficiency of resource utilisation. Values of b greater than unity have been argued to indicate a reduction in the efficiency of resource utilisation as plant density increases.

This reparameterisation has the advantage that it is similar to the changes made for statistical purposes by Gillis and Ratkowsky (1978) and has similarities with the model describing the density dependant net growth rate from generation to generation in insect populations (Hassell, 1975). The basic model for a single insect species population trajectory was developed into a model describing the competitive interactions of two species (Hassell & Comins, 1976) which was later adapted to plant competition (Watkinson, 1981). For two competing species, A and B, in a mixture, the mean yield of species A can be described by the following equation:

$$W_A = W_{mA} (1 + a_A (N_A + \alpha N_B))^{-bA} \qquad \text{(equation 2)}$$

where N is the number of surviving plants at harvest,

α is the competition coefficient or equivalence, representing the number of plants of a second species which have the same effect on the yield of the first species as one individual of the first species.

3.1.5 Experimental investigation of the population growth of the bromes.

Effective management strategies, whether for the control of a weed or the conservation of a rare species, require an understanding of the responses of the species to changes in the habitat in which it grows. If a species is suppressed by the presence of a crop such that the population tends towards extinction, due to insufficient seed production, then that weed will not present a threat in the eyes of a farmer nor will that habitat be suitable for the conservation of that species. Whether *B. interruptus* will persist in cereal fields is unknown.

The aim of the first experiment reported in this chapter was to assess the population growth of the four brome species in conditions that simulate those of an arable field headland. Differences were apparent in the germination biology of the four bromes, as summarised in section 2.9. However, in an arable winter cereal cropping system the husbandry practices used during seed bed preparation and harvesting may obscure some of these differences. Although it has been shown (section 2.8) that the four species disseminated seed at different rates, when grown in wheat, the practice of combine harvesting will, in effect, truncate the natural temporal dispersal patterns of those species that had seed remaining on the plant at the time of harvest. For these species this implies that the dissemination of *B. interruptus* will be greatly hastened by combining, the other three species having shed the majority of seed by the time harvesting occurs (section 2.8). Therefore, the bulk of the seed of these species will be deposited on the soil surface over a short period, between maturity of the grasses and the harvesting of the crop. Although the seed of *B. commutatus*, *B. mollis* and *B. sterilis* may be shed at a faster rate than *B interruptus* it is unlikely that a substantial fraction of these seeds will germinate initially, germination of seeds of these species on the stubble surface having been shown to be protracted (section 2.4). This may, in part, be due to limited water availability (section 2.3). As the field experiment is intended to simulate a field under a minimum tillage system it can be assumed that seed bed preparation will occur soon after harvesting of the previous crop. The soil surface will be disturbed during either seed bed preparation by harrowing or seed drilling by the drill, but not to sufficient depths to prevent seedling establishment (section 2.4). This disturbance of the soil surface will promote the germination of all four species, compared to on the stubble surface, and result in near synchronous germination of all four species.

The range and choice of the treatments used in the simulation of a headland habitat were restricted by the limitations of the resources (land, seed and labour) available for the experiment. Treatments were, therefore, chosen that were considered to be influential determinants of the habitat mosaic, these factors being shown to be important when the wheat density in a cereal field was surveyed (section 1.4). These included variations in wheat density and weed density as well as the effects of vehicle passage on young plants.

The second experiment was an investigation of the competitive interaction of two of the grasses, *B. interruptus* and *B. sterilis.* Conditions favouring either species are liable to be suitable for the other species also and so the outcome of their competitive interaction is of importance in any consideration of a management plan for the reintroduction and conservation of *B. interruptus.*

3.2 Population growth in arable headland habitats - experimental analysis.

In 1987/1988 a field experiment was conducted at the Botanic Gardens, Ness which investigated the seed production of the four brome grasses under a range of situations considered as characteristic of those found in an arable field headland (section 1.5 and 3.1.5). The experiment was conducted on a sandy loam soil.

3.2.1 Materials and Methods

Experimental Design

Experimental treatments applied to all four brome species were factorially arranged across;

1) crop density,

2) weed density,

3) wheeling, by vehicle passage, at a single point in the cropping cycle.

The experimental plots, each 1.5 x 1.5 m, were arranged on a split, split plot randomised block design over two blocks. Figure 3.2.1 illustrates the main and sub plot arrangement. Replication was not uniform as more replicates of the lower densities were used. The lowest density was achieved by regarding four neighbouring plots as one large plot of 9 m^2 in which five single plants were grown, each plant being considered as a single replicate for that density. The densities 1, 10 and 100 seeds m^{-2} were replicated twice within each wheeling/crop sub plot whilst the two higher densities occurred only once per sub plot. The total combination of treatments was replicated completely in the second block, which gave a total of 432 plots.

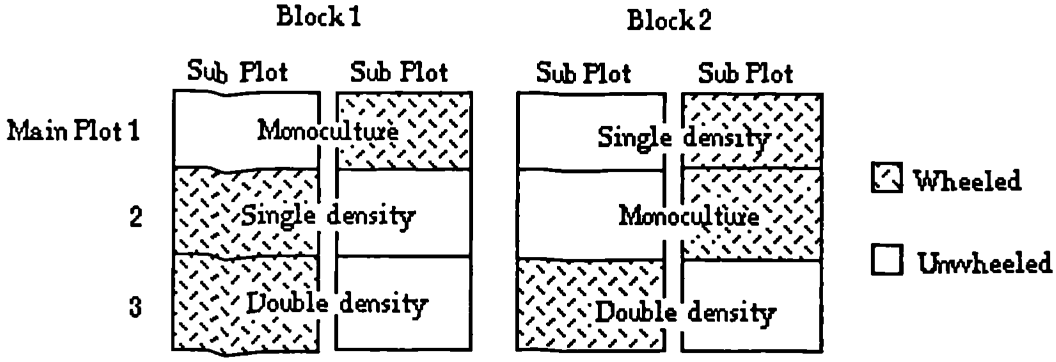
Each wheeling/crop sub plot was divided by three 2.2 m wide paths to allow access for herbicide boom spraying. Further subdivision was by two 0.5 m wide paths parallel to the wide paths and by a 1 m wide path perpendicular to these. Together these paths divided the sub plot into units of four plots allowing reasonable access to all individual plots in the main plots of each block.

The crop was sown at one of two densities either 188 kg ha^{-1}, representing the standard agricultural sowing rate or at 376 kg ha^{-1}, double this standard. One third of the experiment was left unsown with the crop as a control. The crop used was winter wheat cv Avalon. The crop was sown on 5.11.87 using an agricultural seed drill. Afterwards the plots were laid out, their positions being marked with string and canes.

The six weed densities were 0.5, 1, 10, 100, 1,000 and 10,000 seeds sown m^{-2}, extra seed was included to allow for inviability based on the results of a prior germination test (Appendix 2). The grass seeds were sown by hand and lightly raked into the soil surface. The positions of plants at low density were marked with coloured wire rings and the excess seedlings thinned to the required density once established.

The wheeling treatment was applied to half the experimental plots and consisted of a single pass by an Iseki tractor on 3.12.87. The tractor weighed 540 kg and the tyres were approximately 20 cm wide.

Figure 3.2.1 Diagrammatic representation of the arrangement of main and sub plots:- wheat densities and wheeling treatment.



Twenty kg N ha^{-1}, in the form of ICI No3 fertilizer (9:24:24 N:P:K), was incorporated into the seed bed at crop sowing. Subsequent additions were two applications of 70 kg N ha^{-1} as Nitram for the standard density crop and 140 kg N ha^{-1} for the double density. The time at which fertilizer was applied followed conventional winter cereal husbandry, the first application in early March to promote tillering of the crop and the second in late April to encourage tiller survival. All fertilizer applications were broadcast by hand. The monocultures received no fertilizer additions.

Plots were regularly inspected and unwanted weed species removed by hand as and when required. Since hand weeding proved insufficient to control *Poa annua* L., all experimental plots received an application of the herbicide Tolkan (a.i. Isoproturon) at 3.75 l ha^{-1}, by boom sprayer. Prior to treatment the herbicide was tested for its effects on all four brome grasses and found to produce no significant mortality (Appendix 3).

Monitoring.

Monitoring of plant numbers occurred during the experiment as follows;

8.1.88 - wheat density monitored for both sowing rates under both wheeled and unwheeled treatments and in both blocks by taking ten randomly placed quadrats (0.0625 m^2) per treatment combination.

9.2.88 - all species, at all densities, under both wheeled and unwheeled conditions but only in monoculture Block 1.

27.4.88 - 6.5.88 - all species, at all densities, under both wheeled and unwheeled conditions, for both wheat levels and the control, in both blocks.

Harvesting

Plot harvesting occurred as soon as seeds were ripe and was staggered as the timing of maturity differed amongst species and according to density. The harvesting procedure was to place a 1 m^2 quadrat in the centre of each 2.25 m^2 plot thereby avoiding edge effects. From this central quadrat all plants were harvested and the material placed in paper sacks or bags. Counts were made at this time of plant numbers at harvest either by counting all those in the quadrat or, at the higher densities, by using smaller quadrats (0.0625 m^2) and counting remaining plant bases once the seed heads were removed.

All the harvested material was subsequently dried in ovens to prevent rotting prior to being threshed. Threshing was by hand for material from the plots at low densities and by a small motor driven thresher for material from the plots at the higher densities where a greater volume of plant material had to be processed. Seed numbers were estimated from the weight of threshed seeds.

3.2.2 Analysis

Analysis of variance (SAS, 1985), was used to assess the influence of sowing density and wheeling treatment on the crop establishment two months after sowing.

Linear regression analysis of the number of plants (m^{-2}) five months after sowing and plants at harvest against number sown (log transformed) was used to investigate density dependent mortality in the four bromes. Plant densities five months after sowing and at harvest were also analysed by analysis of variance.

The response to density was analysed by fitting the model

$$Ypp = R\,(1 + aN)^{-b} \qquad \text{equation 1}$$

where Ypp is the seed yield per plant and N is the density at harvest. **R** is the maximum seed yield per plant. Data sets, for the four species, were fitted with the model for each wheeling/crop treatment combination, using data meaned across both blocks. Data was log transformed to ensure homogeneity of error variance prior to model fitting using Maximum Likelihood Program, MLP, (Ross, 1987). Seed yield/plant of all four species at the three lowest sowing densities ((0.5, 1 & 10 seeds m^{-2}) was also analysed by analysis of variance.

3.2.3 Results

3.2.3.1 Plant survivorship

Crop

Analysis of variance of seedling survivorship, two months after sowing (Table 3.2.a), showed a significant effect of the wheeling treatment ($P<0.004$) and sowing density ($P<0.0001$). In the absence of the wheeling treatment, the double sowing rate resulted in approximately twice the wheat density (Figure 3.2.2). The wheeling treatment resulted in a reduction of seedling numbers at both densities but the effect was more marked at the double sowing rate wheat. This interaction, between wheeling treatment and sowing density, was statistically significant (P<0.0038). Establishment from the single sowing rate was reduced by wheeling by an average of 11% compared to the unwheeled plots whereas the double sowing rate wheat was reduced by an average of 44%, a four fold difference in effect.

Bromes

Analysis of variance of the plant densities in the spring (April/May 1988) (Table 3.2.d) and at harvest (August, 1988) (Table 3.2.e) showed there to be no significant effect on the survivorship of the grasses caused by the presence of the crop (P>0.05) or the wheeling treatment (P>0.05). Nor was there a significant difference in mean survivorship between the two blocks (P>0.05). At the first monitoring, in the spring, there was a significant difference (P<0.0001) in the overall number of plants amongst the species. There was an average density of 2160 *B. interruptus* plants compared to 1893 *B. mollis* plants and approximately 1500 plants of *B.commutatus* and *B. sterilis*. However, this difference was not apparent at harvest (P>0.05). As expected there were significant differences amongst the sowing densities (P<0.0001).

Plots of plant density in spring (April/May) against sowing density and plant density at harvest against sowing density, on logarithmic scales, were made to investigate density dependence. Linear regression for the spring data, for all four species in monoculture under both wheeling treatments, Table 3.2.b, showed that no density dependent mortality had occurred during seedling establishment and the early phases of growth as none of the regression coefficients were significantly different from one. Regression coefficients calculated on the densities of plants at harvest for all species, wheat levels and treatments, Table 3.2.c, showed six cases of statistical difference from unity. However, plots of these graphs showed that, in all cases, the differences were due to disproportionate loss at the low densities, as illustrated in Figure 3.2.3. Therefore whilst no negative density dependent mortality occurred for any of the species grown within the density range of this experiment, positive density dependence was detected.

3.2.3.2 Seed yields of surviving brome plants.

From Figure 3.2.4 it can be seen that all four species exhibited the same basic trend of declining seed production per plant with increased plant density, under all treatment combinations. The graphs, and the parameter estimates from which the curves were drawn (Table 3.2.f), were based on the mean of all replicates, across both blocks, for each sowing density. Differences were, however, discernible between treatments in the actual yields and the weed densities at which substantial yield reduction occurred. A noticeable feature of the majority of the graphs is the initially gradual rate at which seed yield/plant declined with increased harvest density, upto harvest densities of approximately 100 plants m^{-2}. The exceptions were *B. interruptus* in unwheeled monoculture and *B. mollis* in wheeled and unwheeled monoculture, where a rapid reduction in seed yield/plant was apparent with increase in plant density even at the densities below 100 plants m^{-2}. This gradual decline in yield, over the lower end of the density range, in part, explains why the estimation of the parameters **a** and **b** may not be precise. The lack of a marked response with increasing density in the yield density curves makes estimation of **a** and **b** less precise, resulting in the large standard errors, relative to the estimates themselves, shown for some values of **a** and **b** (Table 3.2.f). Inherent experimental variation also contributes to the lack of precision of these estimates.

Estimation of **R**, the seed yield/plant under no crowding, appeared to be more precise than the estimates of **a** and **b**. In most cases the standard error of **R** was considerably smaller than the estimate itself. In general, good fits were achieved for the meaned data to equation 1, as indicated by the high values of r^2, the coefficient of determination (quoted in Table 3.2.f).

Trends were apparent amongst the estimates of the three parameters **R**, **a** and **b**, for the four species, although there were some differences amongst the four species. All species showed a decline in the value of R with increased wheat density in the unwheeled plots. In the plots that received the wheeling treatment this trend was also apparent for all the species, with the exception of *B. commutatus* where the yield at the double sowing rate of wheat was higher than at the single sowing rate. When yields were compared between

Table 3.2.a Analysis of variance of the number of wheat seedlings surviving two months after sowing. Type III sums of squares used.

Source	d.f.	M.S.	F Ratio	$P_{(Ho)}$
Blocks	1	3.2	<0.001	0.9836
Wheeling (W)	1	102531.2	13.57	0.0004
Sowing density (SD)	1	231555.2	30.64	0.0001
W x SD	1	67280.0	8.90	0.0038
Error	75	7557.2		
Total	79	12255.2		

Table 3.2.b Linear regression coefficients of the relationship between plant density and sowing density (logarithmically transformed data) for the four brome species, in monocultures, at the spring monitoring, April/May 1988.

Species		*B. commutatus*	*B.interruptus*	*B.mollis*	*B.sterilis*
Treatment	Unwheeled (U)	0.9407	1.0343	1.0715	0.9594
	Wheeled (W)	0.9607	1.0199	1.0478	1.0516

All regression coefficients not significantly different from unity (by *t*-test).

Table 3.2.c Linear regression coefficients of the relationship between plant density and sowing density (logarithmically transformed data) for the four brome species, at harvest, August 1988.

Crop	Treatment	Species			
		B.commutatus	*B.interruptus*	*B.mollis*	*B.sterilis*
Monoculture	U	0.9488	1.0423	0.9851	1.0516
	W	0.9256 *	0.9965	1.0042	1.0269
Single Density	U	0.9901	1.0556	1.0204	1.1176 *
	W	0.9524	1.0056	1.0182	1.0435
Double Density	U	0.9554	1.1124 *	1.0137	1.1013 *
	W	1.0158	1.0660 *	0.9782	1.0873 *

* - Significantly different from 1 (P<0.05).

Table 3.2.d Analysis of variance of the number of brome plants (m^{-2}) surviving in April/May 1988. Type III sums of squares used.

Source	d.f.	M.S.	F Ratio	$P_{(Ho)}$
Main Plots				
Block (B)	1	1107021	0.53	NS
Crop (C)	2	2655933	1.28	NS
Main Plot Error	2	2082874		
Sub Plots				
Wheeling (W)	1	132553	0.01	NS
W x C	2	4852021	0.32	NS
Sub Plot Error	3	15361731		
Sub Sub Plots				
Species (Spp)	3	22491156	21.29	0.0001
Sowing Density (SD)	3	1996916400	1890.46	<0.0001
Spp x SD	9	23049677	21.82	0.0001
Spp x C	6	1559742	1.48	0.1839
Spp x W	3	457510	0.43	0.7294
Spp x C x W	6	1063083	1.01	0.4201
SD xC	6	3367564	3.19	0.0044
SD x W	3	41180	0.04	0.9897
SD x C x W	6	4451189	4.21	0.0004
Spp x SD x W	9	491854	0.47	0.8977
Spp x SD x C	18	1912619	1.81	0.0212
Spp x SD x C x W	18	1169710	1.11	0.3405
Sub Sub Plot Error	562	1056314		
Total	663	10649148		

Table 3.2.e Analysis of variance of the number of brome plants (m^{-2}) at harvest. Type III sums of squares used.

Source	d.f.	M.S.	F Ratio	$P_{(Ho)}$
Main Plots				
Block (B)	1	4902615	1.57	NS
Crop (C)	2	3249132	2.08	NS
Main Plot Error	2	3116714		
Sub Plots				
Wheeling (W)	1	1021699	0.92	NS
W x C	2	198066	0.18	NS
Sub Plot Error	3	1116442		
Sub Sub Plots				
Species (Spp)	3	2834795	2.52	0.0576
Sowing Density (SD)	3	1363247600	1214.25	<0.0001
Spp x SD	9	3999526	3.56	0.0003
Spp x C	6	785478	0.70	0.6501
Spp x W	3	1489734	1.33	0.2655
Spp x C x W	6	619733	0.55	0.7683
SD xC	6	343857	3.06	0.0063
SD x W	3	661834	0.59	0.6223
SD x C x W	6	614770	0.55	0.7718
Spp x SD x W	8	1622195	1.44	0.1768
Spp x SD x C	16	1094060	0.97	0.4845
Spp x SD x C x W	16	851307	0.76	0.7325
Sub Sub Plot Error	326	1122706		
Total	423	11866019		

Table 3.2.f Parameter estimates describing the yield/density relationships of the four brome species fitting equation 1, using MLP.

E - estimate SE - standard error U - unwheeled W - wheeled

Species *B. commutatus*

Treatment **Code**			**Parameter**			**Coefficient of determination**
			a	**b**	**R**	$\mathbf{r^2}$
Mono-culture weeds	a) U	E	0.00889	1.16402	893.51	96.77
		SE	0.00669	0.24504	224.67	
	b) W	E	0.03115	0.90947	1244.41	97.87
		SE	0.02380	0.15194	287.43	
Standard Density Wheat	c) U	E	0.00712	1.12426	585.83	96.69
		SE	0.00532	0.24375	137.84	
	d) W	E	0.00583	1.14462	472.48	96.79
		SE	0.00409	0.25353	95.23	
Double Density Wheat	e) U	E	0.00048	2.76717	111.50	95.89
		SE	0.00001	0.33063	20.01	
	f) W	E	0.01034	1.00250	541.33	97.16
		SE	0.00960	0.24577	117.17	

Species *B. interruptus*

Treatment **Code**			**Parameter**			**Coefficient of determination**
			a	**b**	**R**	$\mathbf{r^2}$
Mono-culture weeds	a) U	E	0.01165	2.39906	831.08	99.04
		SE	0.00959	0.84928	197.68	
	b) W	E	0.00515	1.37464	772.79	98.67
		SE	0.00185	0.16140	129.30	
Standard Density Wheat	c) U	E	0.00837	0.98666	418.66	99.06
		SE	0.00389	0.12568	46.80	
	d) W	E	0.00352	1.11358	311.30	94.18
		SE	0.00203	0.24780	72.44	
Double Density Wheat	e) U	E	0.00446	0.88340	130.20	96.05
		SE	0.00214	0.15247	18.32	
	f) W	E	0.00429	1.06450	250.00	99.86
		SE	0.00050	0.04123	9.36	

Table 3.2.f continued

Species *B. mollis*

Treatment				Parameter		Coefficient of determination
Code			a	b	R	r^2
Mono-culture weeds	a) U	E	0.10160	0.94994	2436.55	98.82
		SE	0.09007	0.12897	739.17	
	b) W	E	0.17813	0.80460	2049.56	99.76
		SE	0.06609	0.04219	259.68	
Standard Density Wheat	c) U	E	0.00864	1.06773	422.65	95.26
		SE	0.01048	0.34306	124.49	
	d) W	E	0.01037	1.05678	433.93	96.50
		SE	0.01023	0.26084	115.60	
Double Density Wheat	e) U	E	0.01878	0.92929	310.96	98.93
		SE	0.01101	0.19274	44.13	
	f) W	E	0.00789	0.97655	225.77	94.07
		SE	0.01154	0.39017	65.10	

Species *B. sterilis*

Treatment				Parameter		Coefficient of determination
Code			a	b	R	r^2
Mono-culture weeds	a) U	E	0.13007	0.86432	1014.89	98.45
		SE	0.13503	0.13292	330.73	
	b) W	E	0.09275	0.92160	1072.64	98.67
		SE	0.07246	0.11935	283.91	
Standard Density Wheat	c) U	E	0.08463	0.74055	479.38	99.60
		SE	0.03734	0.05441	53.99	
	d) W	E	0.03874	0.88428	551.71	98.36
		SE	0.03738	0.16908	121.31	
Double Density Wheat	e) U	E	0.07608	0.72624	226.53	97.61
		SE	0.07331	0.12432	55.88	
	f) W	E	0.05324	0.79570	400.17	96.13
		SE	0.04814	0.14358	95.54	

Table 3.2.g Analysis of variance of the seed yield/plant for the four brome species, grown at the three lowest sowing densities (0.5, 1 & 10 seeds m^{-2}), at both crop densities and in monoculture, under both wheeled and unwheeled treatments. Type III sums of squares used.

NS - Not significant (P>0.05) * Signifcant (P<0.05) ** Signifcant (P<0.01) *** Signifcant (P<0.001)

At a sowing density of 0.5 seeds m^{-2}

Source	d.f.	M.S.	F Ratio	$P_{(Ho)}$
Main Plot				
Block (B)	1	1595488	152.05	**
Crop (C)	2	20683349	1971.11	***
Main Plot Error	2	10493		
Sub Plots				
Wheeling (W)	1	550739	0.29	NS
W x C	2	307251	0.16	NS
Sub Plot Error	3	1880414		
Sub Sub Plots				
Species (Spp)	3	2472713	7.35	0.0001
Spp x C	6	1516394	4.51	0.0003
Spp x W	3	651475	1.94	0.1259
Spp x C x W	6	784548	2.33	0.0348
Sub Sub Plot Error	157	336387		
Total	186	693876		

At a sowing density of 1 seeds m^{-2}

Source	d.f.	M.S.	F Ratio	$P_{(Ho)}$
Main Plots				
Block (B)	1	1316260	13.8	NS
Crop (C)	2	13183347	138.32	**
Main Plot Error	2	95310		
Sub Plots				
Wheeling (W)	1	573688	9.2	NS
W x C	2	1480384	23.73	*
Sub Plot Error	3	62391		
Sub Sub Plots				
Species (Spp)	3	4034336	26.37	0.0001
Spp x C	6	3296944	21.55	0.0001
Spp x W	3	1694399	11.07	0.0001
Spp x C x W	6	420648	2.75	0.0149
Sub Sub Plot Error	136	153005		
Total	165	571348		

Table 3.2.g Continued

At a sowing density of 10 seeds m^{-2}

Source	**d.f.**	**M.S.**	**F Ratio**	**P$_{(Ho)}$**
Main Plots				
Block (B)	1	2011908	12.58	NS
Crop (C)	2	5172879	32.35	*
Main Plot Error	2	159902		
Sub Plots				
Wheeling (W)	1	8422	0.06	NS
W x C	2	271705	1.84	NS
Sub Plot Error	3	147348		
Sub Sub Plots				
Species (Spp)	3	1031081	11.66	0.0001
Spp x C	6	770776	8.72	0.0001
Spp x W	3	732917	8.25	0.0001
Spp x C x W	6	853362	9.65	0.0001
Sub Sub Plot Error	62	88442		
Total	91	361323		

Figure 3.2.2 The effect of the wheeling on crop establishment in relation to sowing rate, one month after treatment.

LSD (P<0.05) = 27.49

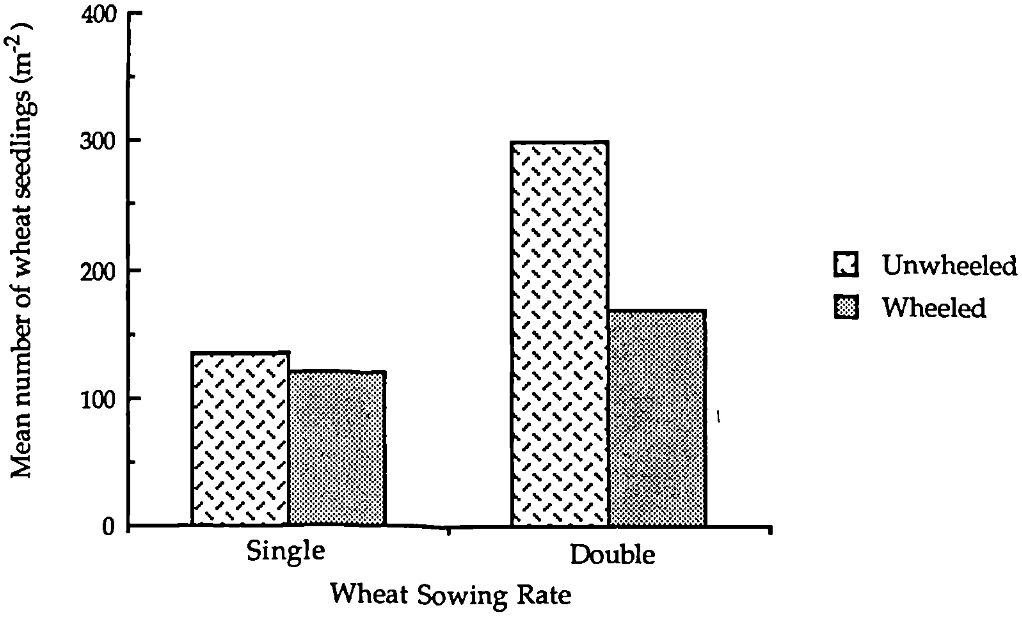


Figure 3.2.3 The relationship between sowing density (seeds m^{-2}) and harvest density (plants m^{-2}) for *B. sterilis* grown in wheat (sown at 376 kg ha-1) in the absence of the wheeling treatment.

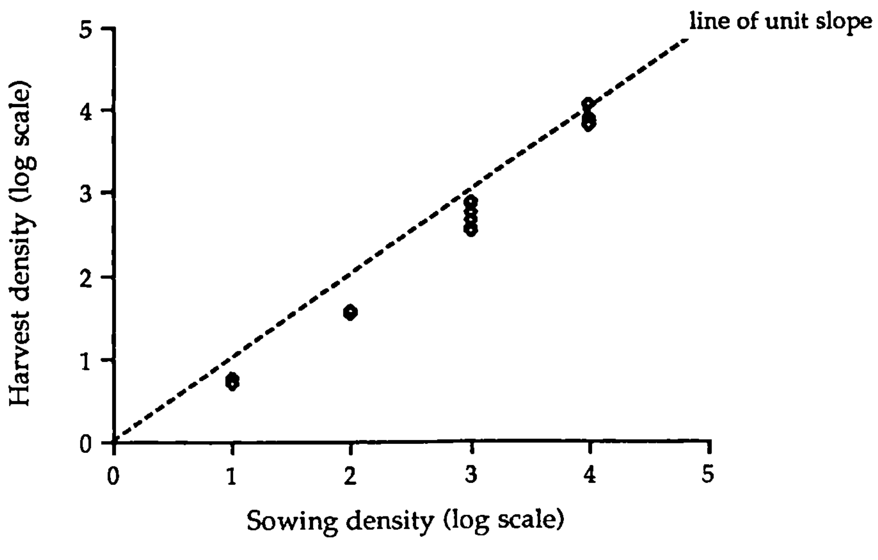


Figure 3.2.4. Yield/density relationships for all four brome species, in all crop and wheeling treatment combinations, as annotated below. Curves fitted to data meaned over all replicates and both blocks using parameter estimates given in Table 3.2.f.

a) In monoculture - unwheeled
b) In monoculture - wheeled

c) In wheat at single sowing rate - unwheeled
d) In wheat at single sowing rate - wheeled

e) In wheat at double sowing rate - unwheeled
f) In wheat at double sowing rate - wheeled

Figure 3.2.4 continued

B. commutatus

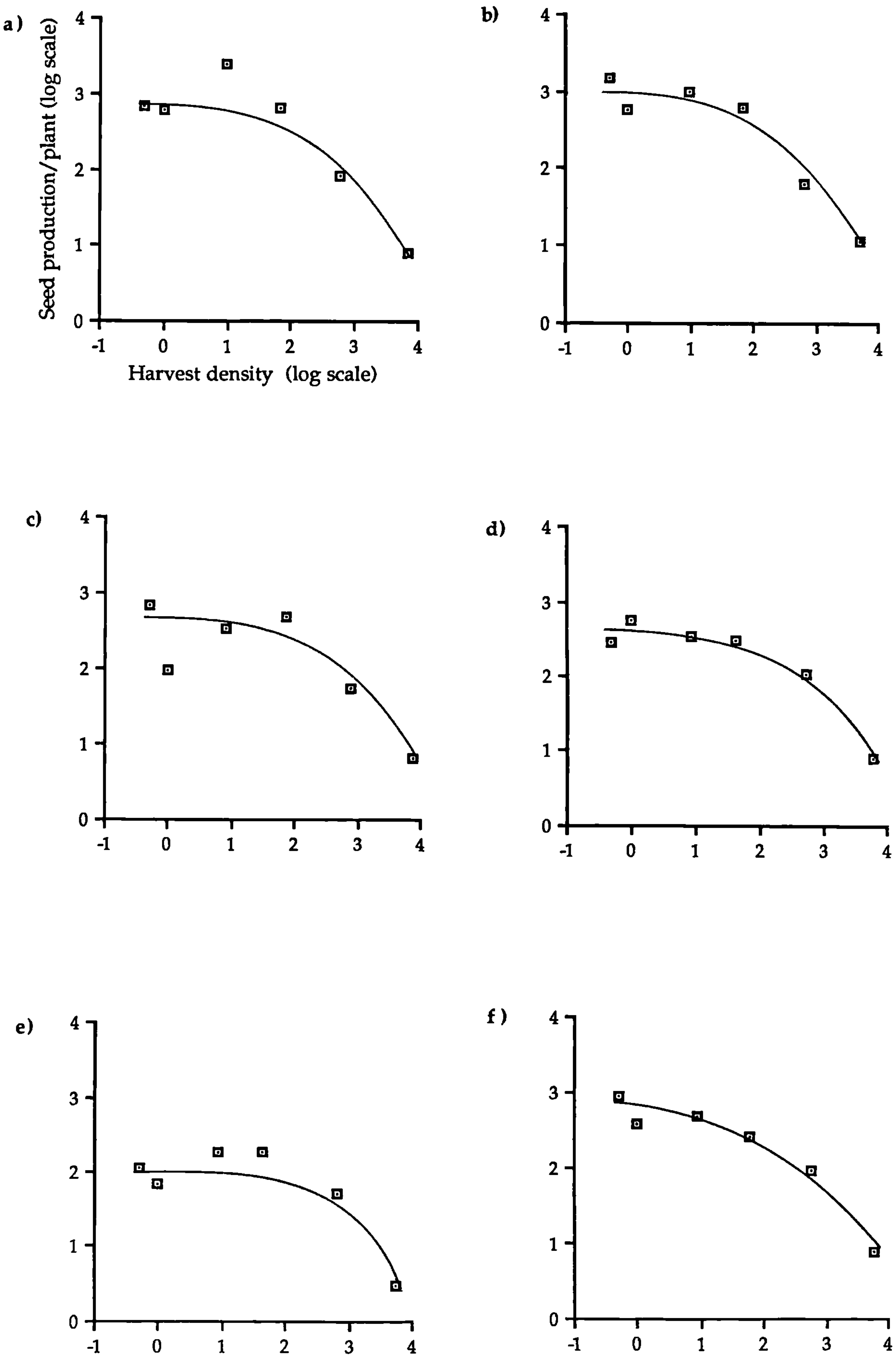


Figure 3.2.4 continued

B. interruptus

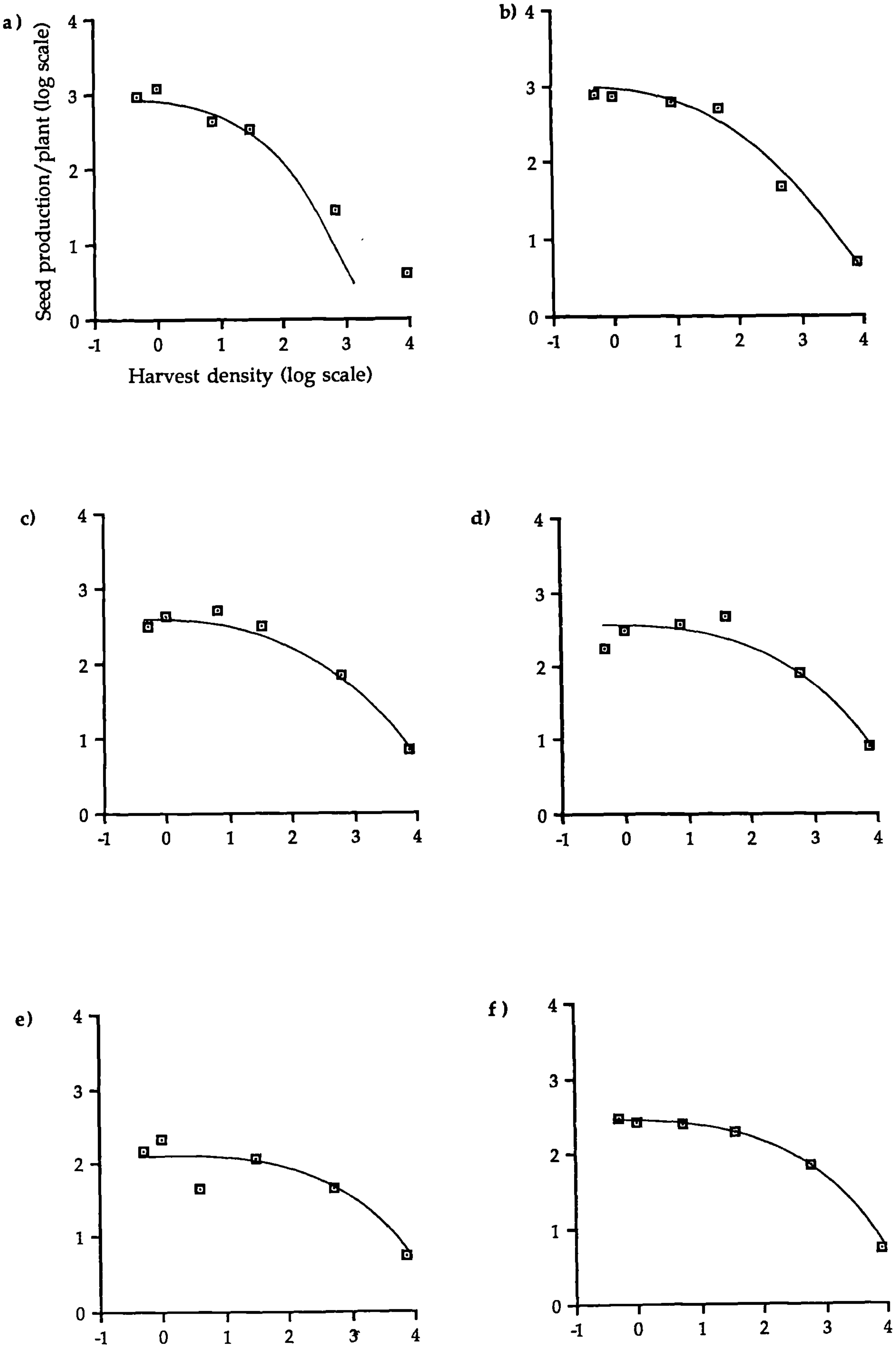


Figure 3.2.4 continued

B. mollis

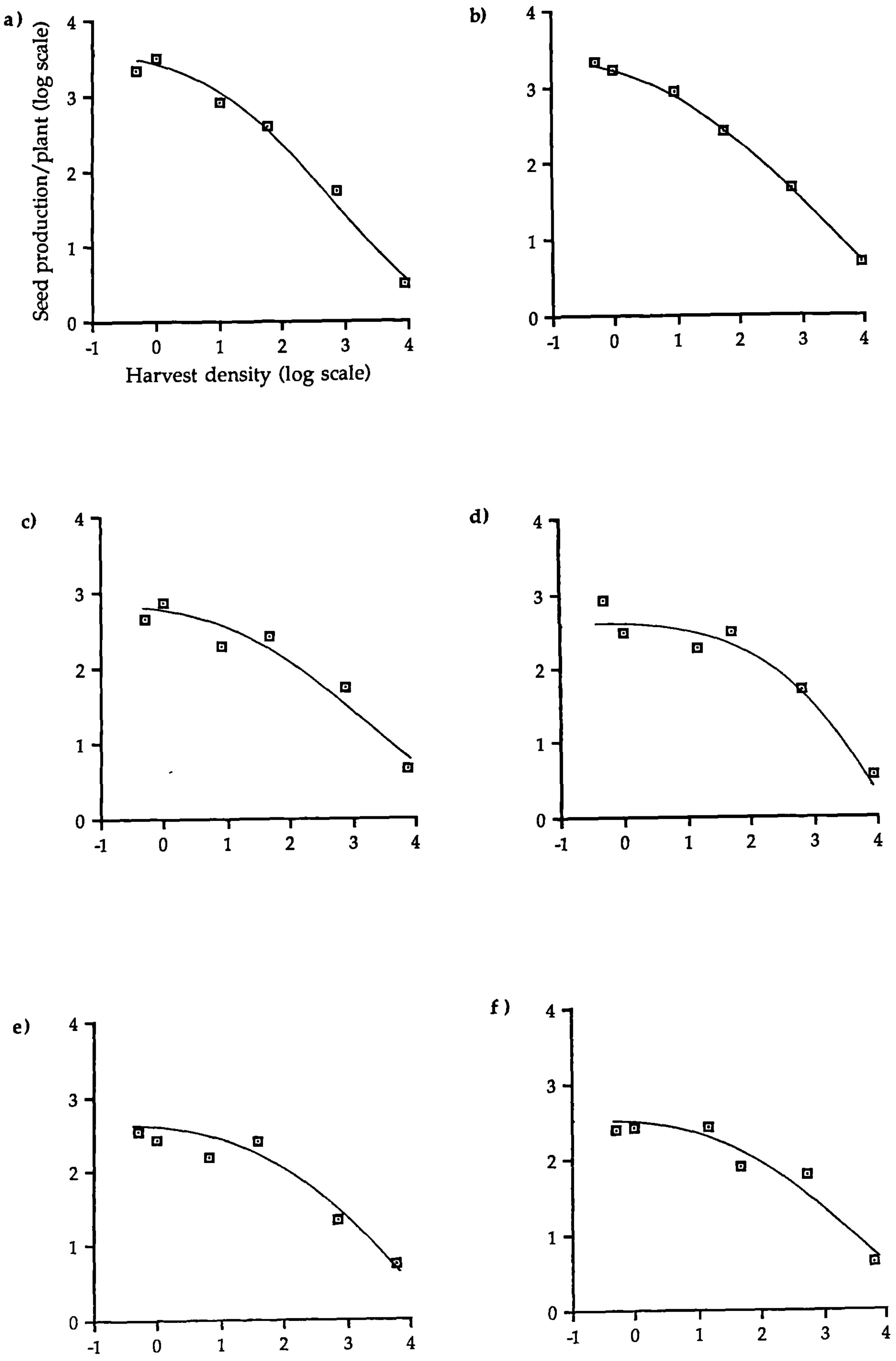


Figure 3.2.4 continued

B. sterilis

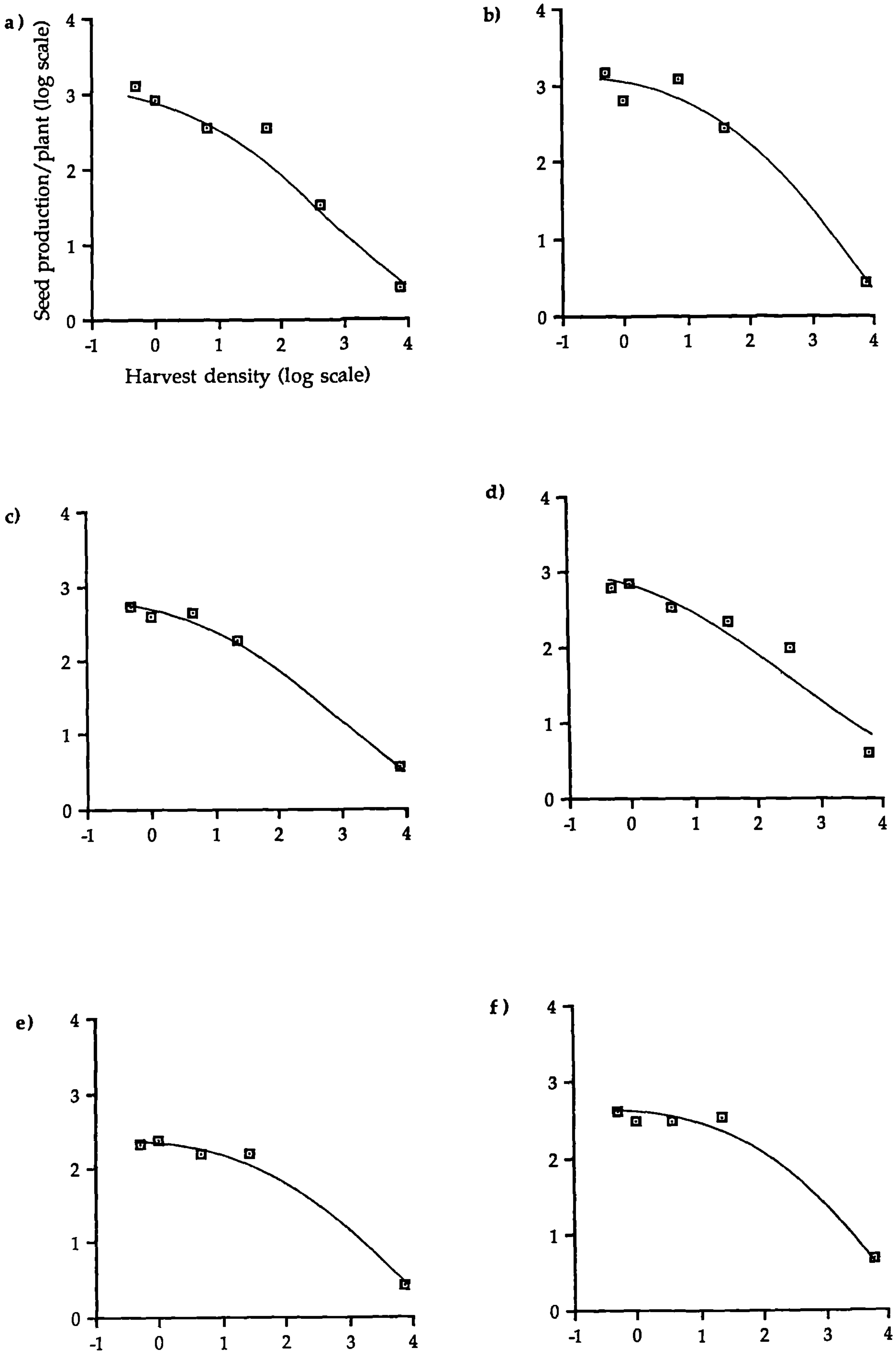
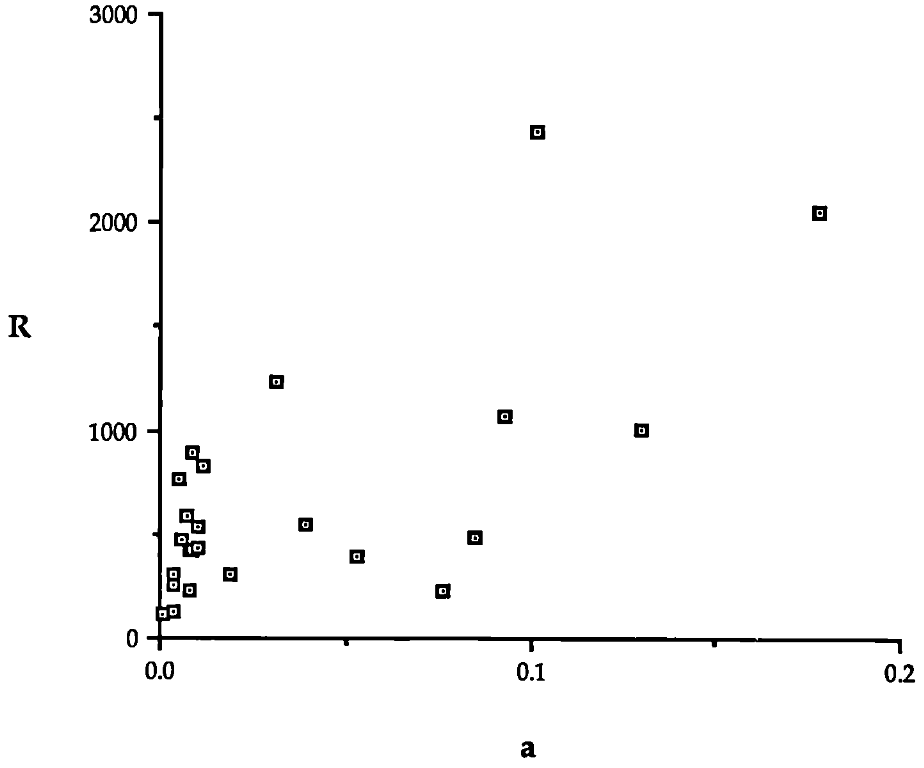


Figure 3.2.5 The relationship between parameter estimates of R and a for the four brome species under all treatments (Values of R and a from Table 3.2.f)



treatments at the same wheat density all species showed similar or lower seed yields under the wheeling treatment when grown in monoculture and single density wheat. However, at the double density wheat the yields were higher under the wheeling treatment than in the unwheeled plots with the exception of *B. mollis*, which exhibited lower yields in the wheeled plots. This indicated a species x crop x wheeling interaction.

Further evidence of this interaction is apparent in the analysis of variance of the seed yields/plant at the three lowest sowing densities (0.5, 1 and 10 seeds m^{-2}) (Table 3.2.g) where the species x crop x wheeling interaction was significant in all cases ($P<0.0348$, $P<0.0149$ and $P<0.0001$, respectively). These analyses of variance also showed that there were significant differences in the yields amongst the species ($P<0.0001$ at all three sowing densities) and emphasised the effect of the wheat density on yield reduction as the crop presence was significant at the sowing densities of 0.5, 1 and 10 seeds m^{-2} ($P<0.001$, $P<0.01$ and $P<0.05$, respectively).

Trends were also apparent in the estimates of **a**, the reciprocal of which is the density at which interference between neighbours becomes appreciable (Table 3.2.f). For *B. commutatus*, *B. interruptus* and *B. sterilis* there was a trend of diminishing values of **a** with increasing wheat density in the unwheeled plots whereas *B.mollis* showed no trend in values of **a** under this treatment. In wheeled plots *B. commutatus* showed a trend of increasing values of **a**, *B. interruptus* and to a lesser extent *B. sterilis* showed similar values with no marked trend and *B.mollis* exhibited a marked decline in **a** with increased wheat density. Comparing between the wheeling treatments, across all species, no obvious trend was apparent. A scatter plot of corresponding values of **R** and **a** (Figure 3.2.5) showed no strong correlation between the estimates of these two parameters.

Comparisons of the estimates of **b**, as with **a**, can be made but the large standard errors for the estimates of both these parameters must be borne in mind, limiting the credibility of any trends apparent. For *B. commutatus* all the estimates of **b** were close to or larger than unity with the exception of the unwheeled, double wheat density plots. The estimates of **b** for *B. interruptus* and *B.mollis* were close to and spanned unity with the exception of *B. interruptus* in unwheeled monoculture where a high estimate (2.399) of **b** was produced. Values of **b** for *B. sterilis* were all similar and all below unity.

3.2.4. Discussion

3.2.4.1 Population regulation

Palmbald (1968) stated that density dependent regulation of population size could be controlled in three ways;

1) by self controlled germination (e.g. *Bromus inermis* Leyss) where the proportion of seeds germinating decreases with increased density of seeds.

2) mortality of individual plants (e.g. *Plantago major* L.)

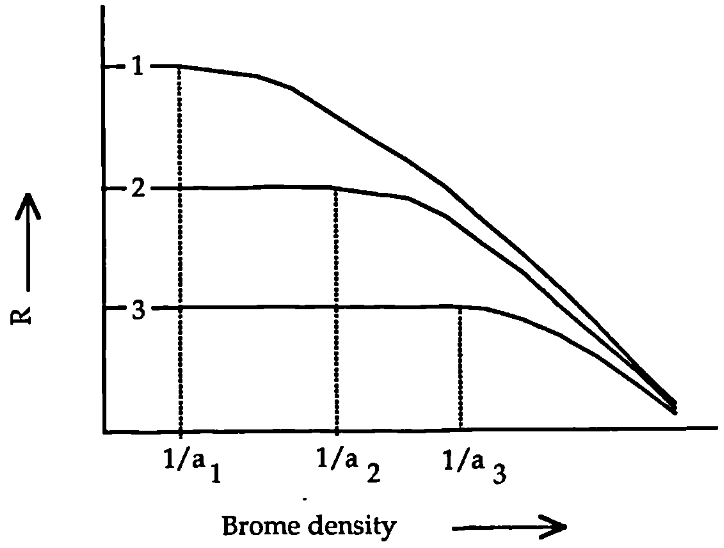
3) via individual plasticity (e.g. *Bromus tectorum* L.) where the numbers of seeds produced per plant is negatively correlated with plant density.

Work on *Agrostemma githago* (Watkinson, 1980; 1981b) showed that a combination of these control mechanisms was possible and both plasticity and mortality may interact as regulatory processes. No density dependent germination or mortality was evident for any of the brome species within the range of densities used in this experiment, therefore density dependent regulation that occurred could only be via plastic changes in individual fecundity. As was clearly shown, the mean seed yields per plant declined providing evidence of plasticity in seed yield. Such regulation via fecundity has a delayed affect, the response being evident in the population numbers in the following generation (Silvertown,1987). The lack of any density dependent mortality shown in this experiment implies that the mortality that did occur was density independent. Even at the highest sowing density, 10,000 seeds m^{-2}, density dependent mortality was not recorded which indicated that the plants had not achieved the size and density at which self thinning would occur (Watkinson, 1981a). Positive density dependence was noted in some cases but no biological explanation can be offered for these results other than the possibility of microclimatic effects favouring plant survival at the higher densities. Alternatively, these results may be the product of experimental variation.

3.2.4.2 Brome yields

The reduction of crop yields due to the presence of weed infestations has been well documented (e.g. Willey & Heath, 1969; Roberts *et al.*, 1982). Some investigations of the population dynamics of weeds have included the effects of crop presence on the weed yields (e.g. Watkinson,1981; Firbank *et al.*,1984). The results of this study also showed that the presence of a wheat crop caused a reduction in weed yields. Based on the results recorded for *B. interruptus* (section 3.2.3.2) certain trends were apparent in the seed yield/plant relationship under increasing wheat density as illustrated below in Figure 3.2.6, a hypothetical graph of this relationship.

Figure 3.2.6 A hypothetical seed yield/density relationship for a brome species, plotted on log/log axes. Curves 1, 2 and 3 represent increasing wheat density in which the brome was grown.



The curves 1, 2 and 3 represent the effect of increasing wheat density on the seed yield/plant. Values of R decrease with increasing wheat density, as shown by all the species in the unwheeled plots (Figure 3.2.4). This decrease was due to interspecific competition from the wheat suppressing the yields of the bromes. Considering each curve separately, i.e. each wheat density, it can also be seen that the size of seed yield/plant declines with increased brome density (as shown in Figure 3.2.4) which would be due to increased intraspecific competition reducing the yield of individual plants.

With the exception of *B. mollis,* the bromes exhibited higher yields under the wheeling treatment at the double wheat sowing rate than in the unwheeled plots. This effect was due to the marked influence that the wheeling treatment had on the survivorship of the wheat at the higher sowing rate (section 3.2.3.1). Reduction in the wheat survivorship, due to the wheeling treatment, reduced the competitive effect of the wheat on the bromes and hence resulted in higher seed yields per brome plant. This effect would also be expected, though to a lesser extent, at the single sowing rate wheat where reduction in the survivorship of the wheat was also detected but less marked (an 11 % reduction in survivorship compared to 44 % for the double density wheat). However, this effect was not apparent which may indicate that the reduction in wheat survivorship was insufficient to increase the brome yields or the response may have been masked by experimental variation within the results. The bromes were not directly influenced by the wheeling treatment as they had not emerged at the time of the treatment being applied whereas the wheat seedlings were at the single leaf stage and approximately 6 cm tall.

The reciprocal of parameter **a** corresponds to the weed density at which interference between neighbouring plants becomes appreciable (Watkinson, 1980). Considering the influence of increasing wheat density on estimation of **a** for *B. interruptus,* from Figure 3.2.5 it appears that increased wheat density would increase the value of 1/a. This implies that the density at which intraspecific competition becomes appreciable increases with increased wheat density. This may be due to the relatively greater importance of interspecific competition from the wheat on the brome yield than intraspecific competition. Investigation of the competitive relationship between *B. interruptus* and wheat supports this argument (Howard *et al.,* 1989).

The value of **a** itself, represents the area required to produce a plant of yield **R**, therefore it appears that with increased wheat density larger areas are required to produce maximum individual plant yield. This implies that a correlation between **R** and **a** may be expected. However, the graph of corresponding values of **R** and **a** for all the species, under all the treatments (Figure 3.2.5) showed the lack of a strong correlation. The lack of a correlation between these parameters may be due to changes in resource utilization or capture under conditions of increased density. Values of **a** can also be expected to vary between species due to differences in plant morphology and growth requirements. Alternatively, the occurrence of a correlation may be obscured by the lack of precision of the parameter estimates.

Not all the species followed this set of trends as presented for *B. interruptus*. *B. commutatus* showed similar trends in the responses of R and **a** to changes in wheat and brome density. *B. mollis* was dissimilar in that the increase in seed yield/plant in the wheeled, double wheat sowing rate plots was not apparent. *B. mollis* was also dissimilar to the other three species in that the estimates of **a** for the wheeled plots decreased with increased wheat density whereas the other species exhibited similar or increasing values of **a** in these conditions. This implies that for *B. mollis* the density at which interference between neighbours becomes appreciable decreased with increasing wheat density. *B. sterilis* was exceptional in that values of R were higher in the wheeled plots at all wheat densities but the overall trends were similar to those for *B. interruptus*.

The precision with which a species responds to changes in its density varies between species. The parameter b, provides an indication of a species ability to compensate for changes in density. If equal to unity parameter **b** indicates that exact compensation has occurred where changes in density have been precisely regulated for by changes in mortality or fecundity. Theoretically, if this were the case, population numbers would remain constant from one generation to the next. Assuming all other parameters remain constant, values of **b** greater than one indicate over compensation where the regulatory measures are so severe that a decline in population numbers results. Conversely values of b less than one represent under compensation where insufficient regulation occurs and population numbers continue to rise.

Although the estimates of **b** had large standard errors (Table 3.2.f) the trends amongst the species are worth mentioning here. For *B. commutatus* there appeared to be a tendency to overcompensate for density, values of **b** being equal to or greater than unity. *B. interruptus*.and *B. mollis* exhibited values of **b** spanning unity which indicated exact compensation although the values of **b** for *B. interruptus*.in monoculture were both greater than unity which implied overcompensation and hence a change in response to density when grown in the presence of wheat. For *B. sterilis* all estimates of **b** were below unity which implies that this species undercompensates for changes in density.

Variation in the yields, and hence the need to use meaned data, were partly due to the variations in the field conditions which were unavoidable considering the large scale of this experiment. During the experiment differences in the drainage of the soil were at times evident, puddling occurring in several places which may well have had detrimental effects on yields. There were other apparent macroscale differences such as a difference in slope between the areas of Block 1 and 2, and in the prior use of the area used. Microscale differences also occurred due to rabbit and squirrel damage which was evident in some plots. Such obvious damage was recorded and aberrant data points removed from the data sets where justified.

3.2.4.3 Implications of these results in relation to population growth in headland conditions.

From Figure 3.2.4 it is apparent that the number of seeds produced per plant was considerably greater than one, for all four species, under all the treatment combinations. In view of the high levels of germination shown in the first four experiments in Chapter 2, population growth could be expected by all four species in conditions similar to those investigated in this experiment, assuming no control methods were used. The use of herbicides effective against these grasses or the practice of mould-board ploughing as part of seed bed preparation are just two factors that could restrict population growth by the reduction of plant survivorship or emergence, respectively, and consequently seed production per unit area.

The presence of the wheat crop was shown to reduce the seed yields of all four brome species and this effect was marked at the low brome densities. The implication of this finding is that the rate of growth of populations of the brome grasses will be greatest in areas of low wheat density. It has been shown (Figure 1.5.1) that the headland of a cereal field has a patchy distribution of wheat densities due to both the drilling pattern of the crop and the detrimental effects of vehicle pressure on the cereal seedlings. In the experiment reported here and in section 2.6 it was shown that the brome species (in the conditions investigated) could tolerate light vehicle pressure without reduced seed yields. This implies that, in theory, these species could exploit the patchy cereal distribution of a headland expanding in the areas of low cereal density that exist and maintaining populations even in the higher crop densities that were evident where double sowing had occurred.

3.3 Competition between *B. interruptus* and *B. sterilis.*

A pot experiment was conducted, in a polythene tunnel house, to investigate competitive interactions between *B. interruptus* and *B. sterilis.*

3.3.1 Materials and Methods

Each species was grown over a range of six densities, from 0 - 5500 seeds m^{-2}, in pairwise combination, giving a total of 36 combinations (see Figure 3.3.1). Two complete replicates were arranged as separate blocks, the location of pots within each block being completely randomised. In an attempt to minimise edge effects large pots were used thereby reducing the proportion of the plants which gained any advantage from exterior positioning. Pots were also positioned closely within blocks further reducing the edge effects due to lateral illumination of plants at the edge of pots.

The pots had an area of 0.26 m^2 and contained 0.026 m^3 low nutrient compost. This was ameliorated by the addition of 0.013 m^3 of John Innes seed compost. Seeds were sown evenly across the surface then covered by 10 mm compost.

The sowing rates were as follows;

Seed m^{-2}	0	4	35	275	2200	5500
Numbers of seeds per pot	0	1	9	72	575	1400

At the lowest density four seeds were sown and thinned to one per pot once established. The plants at low density were ringed for identification purposes. All pots were planted on 28.11.89 and germination appeared complete by 8.1.90. Plants at high density were supported by a network of strings and canes after six weeks growth. Fertilizer, at a rate of 75 kg N ha^{-1} Nitram, was applied to all pots on 30.1.90. Pesticides were applied as required, namely Nimrod T, containing the active ingredients Bupirimate and Triflorine to control mildew and Pirimor to control aphids.

The numbers of seedlings established in all pots were recorded, Block 1 on 16.1.90 and Block 2 on 22.1.90. Harvesting occurred once the plants had set seed and hence were easily distinguishable. At harvest the number of surviving plants were counted and then biomass was recorded after drying to constant weight.

Figure 3.3.1 Diagram of the pairwise sowing combinations (*) used in the experiment.

Sowing	5500	*	*	*	*	*	*
density	2200	*	*	*	*	*	*
of	275	*	*	*	*	*	*
B. interruptus	35	*	*	*	*	*	*
(seeds m^{-2})	4	*	*	*	*	*	*
	0		*	*	*	*	*
		0	4	35	275	2200	5500

Sowing density of *B. sterilis* (seeds m^{-2})

3.3.2 Analysis

The plant densities at harvest, for each species, were plotted against sowing density on log/log axes to indicate if density dependent mortality had occurred (section 3.2.2). Plant densities, at harvest, were log transformed prior to linear regression analysis. Biomass/plant data was analysed using the two equations that form the model described earlier (section 3.1.4) and in Table 3.3.b. Data was log tranformed to normalise the error variance. Both equations were fitted using SAS program NONLIN (SAS, 1985).

3.3.3 Results

Regression analysis showed that density dependent mortality occurred for both species, both in monoculture and in the mixtures (Table 3.3.a). With one exception, *B. interruptus* in mixture with *B. sterilis* sown at a density of 2200 seeds m^{-2}, all regression lines showed significant departure from the line of unit slope ($P<0.05$) (Table 3.3.a). From Figure 3.3.3 it can be seen that for *B. sterilis*, over the whole range of *B. interruptus* sowing densities, density dependent mortality was occurring only at the two highest sowing densities of *B. sterilis*, namely 2200 and 5500 seeds m^{-2}. There appeared to be no response in the density dependent mortality shown by *B. sterilis* to increased sowing density of *B. interruptus* when grown in mixture.

However, from Figure 3.3.2 it can be seen that the density dependent mortality of *B. interruptus* was influenced by the sowing density of *B. sterilis* with which it was in mixture. In monoculture and at the lowest sowing densities of *B. sterilis* (4 and 35 seeds m^{-2}) density dependent mortality of *B. interruptus* appeared to occur only at the two highest *B. interruptus* sowing densities (2200 and 5500 seeds m^{-2}). At the higher sowing densities of *B. sterilis* the mortality of *B. interruptus* was greater, departure from the line of unit slope being apparent at lower *B. interruptus* densities. At the two highest *B. sterilis* sowing densities mortality of *B. interruptus* was marked with no clear trend of increasing density dependent mortality with increased sowing density of *B. interruptus.*

The effects of increasing density, of both species in mixture, on biomass/plant are shown in Figures 3.3.4 and 3.3.5. In monocultures, for *B. interruptus* the reduction in biomass/plant was most noticeable at densities of 275 plants m^{-2} and above whilst *B. sterilis* showed a reduction at 33 plants m^{-2} and all densities above that. For both species an increase in sowing density resulted in reduction of biomass/plant. The effect of increased sowing density of *B. sterilis* had a marked effect on the biomass/plant of *B. interruptus* the relative reductions, however, becoming less as the density of *B. interruptus* increased. At the lowest *B. interruptus* sowing density (4 seeds m^{-2}) no plants survived to harvest and therefore weighing, at both the two highest *B. sterilis* sowing densities (2200 and 5500 seeds m^{-2}). At the second lowest *B. interruptus* sowing density (33 seeds m^{-2}) no plants survived to harvest in the highest *B. sterilis* density.

The effects of increased sowing density of *B. interruptus* on the biomass/plant of *B. sterilis* (Figure 3.3.5) were reduced as the sowing density of *B. sterilis* increased. At the highest two sowing densities of *B. sterilis* (2200 & 5500 seeds m^{-2}) there was little effect of increased sowing density of *B. interruptus.* At all sowing densities of *B. interruptus, B. sterilis* produced plants that survived through to harvest. These results indicate clearly that *B. sterilis* was the stronger competitor in the mixtures of both species.

Table 3.3.a Linear regression coefficients of the relationship between sowing density and harvest density for *B. interruptus* and *B. sterilis* in mixtures.

Sowing density of *B. sterilis* (seeds m^{-2})	**Regression coefficient of *B. interruptus***	**Standard error**	***t***	
0	0.8771	0.0202	6.15	*
4	0.8904	0.0404	2.75	*
35	0.8667	0.0215	6.05	*
275	0.8689	0.0358	3.64	*
2200	0.8394	0.1351	1.19	
5500	-0.0338	0.0110	89.91	*

Sowing density of *B. interruptus* (seeds m^{-2})	**Regression coefficient of *B. sterilis***	**Standard error**	***t***	
0	0.9115	0.0189	4.63	*
4	0.9053	0.0251	3.80	*
35	0.9105	0.0169	5.20	*
275	0.9152	0.0340	2.50	*
2200	0.9101	0.0263	3.46	*
5500	0.9068	0.0346	2.65	*

t (P = 0.05) for 8 degrees freedom = 2.31

* - Significantly different from unity (P = 0.05)

Table 3.3.b Parameter estimates from the fits of biomass/plant data for *B. interruptus* and *B. sterilis* grown in mixtures, over a range of densities, to the model given below;

$$\text{Biomass}_{Bi} = \textbf{Biomass}_{mBi} \, (1 + a_{Bi} \, (N_{Bi} + \alpha \; N_{Bs})) ^{- b_{Bi}}$$

$$\text{Biomass}_{Bs} = \textbf{Biomass}_{mBs} \, (1 + a_{Bs} \, (N_{Bs} + \beta \, N_{Bi})) ^{-b_{Bs}}$$

where **Biomass$_m$** is the biomass of an isolated plant,

a is the approximate area required to produce a plant of biomass$_m$,

b is a measure of resource utilisation,

N is the plant density at harvest,

α is the equivalence that represents the number of *B. sterilis* plants which have the same effect on the yield of *B. interruptus* as one *B. interruptus* plant and β is the equivalence that represents the number of *B.interruptus* plants which have the same effect on the yield of *B. sterilis* as one *B. sterilis* plant (Watkinson, 1980).

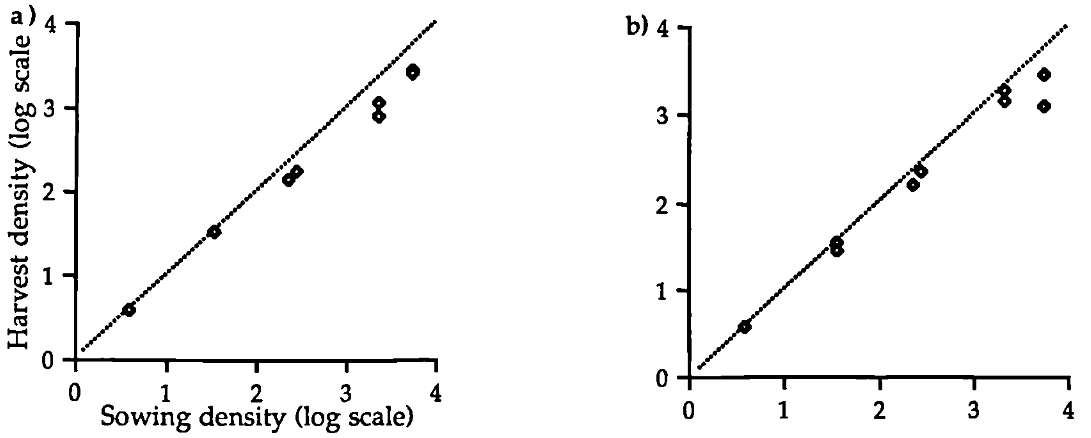
Estimates of parameters describing *B.interruptus.*

Parameter		**Estimate**	**Standard error**
Biomass$_{mBi}$	(g)	23.8172	2.1440
b_{Bi}		1.0450	0.1076
a_{Bi}	(m^{-2})	0.0307	0.0249
Equivalence (α)		6.5134	1.9129

Estimates of parameters describing *B. sterilis*

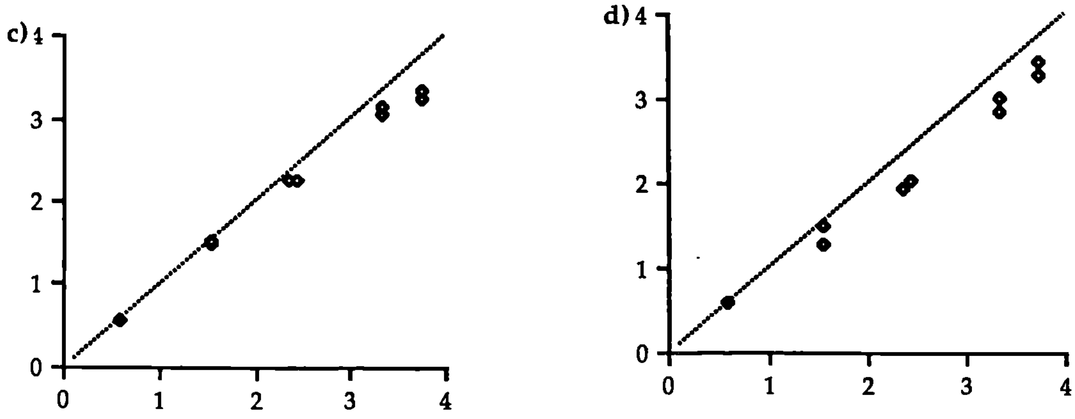
Parameter		**Estimate**	**Standard error**
Biomass$_{mBs}$	(g)	73.7112	15.4185
b_{Bs}		0.9506	0.0460
a_{Bs}	(m^{-2})	0.0989	0.0400
Equivalence (β)		0.1048	0.0164

Figure 3.3.2 The relationship between sowing density and harvest density for *B. interruptus* grown in monoculture and in mixture with *B. sterilis*, at differing densities.



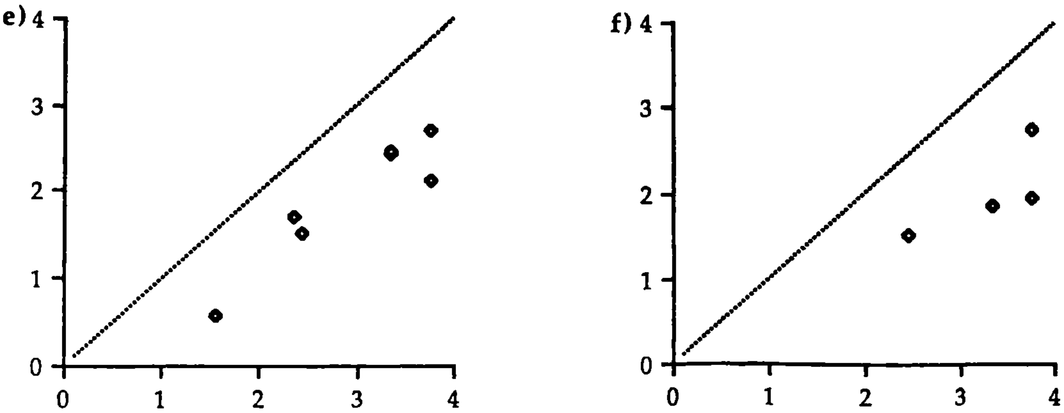
Monoculture

B. sterilis sowing density = 4 seeds m^{-2}



B. sterilis sowing density = 35 seeds m^{-2}

B. sterilis sowing density = 275 seeds m^{-2}



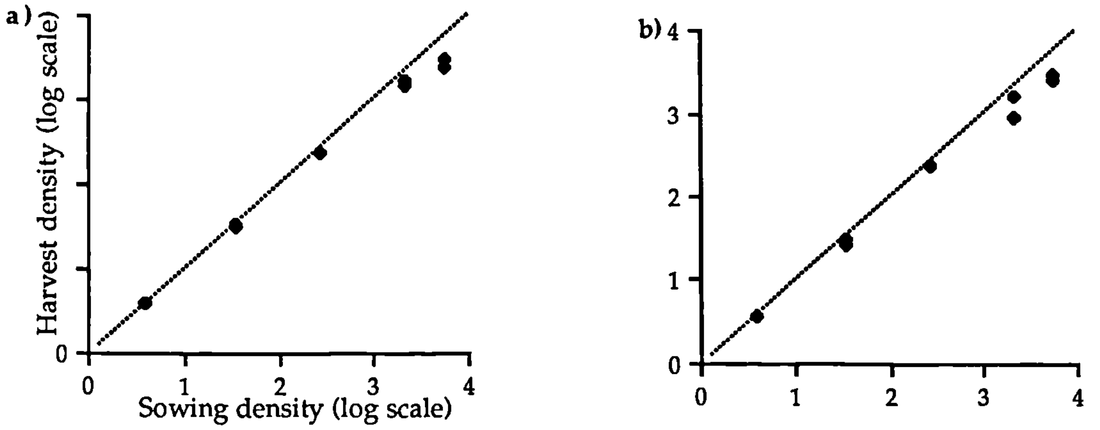
B. sterilis sowing density = 2200 seeds m^{-2}

B. sterilis sowing density = 5500 seeds m^{-2}

Figure 3.3.3 The relationship between sowing density and harvest density for *B. sterilis* grown in monoculture and in mixture with *B. interruptus*, at differing densities.

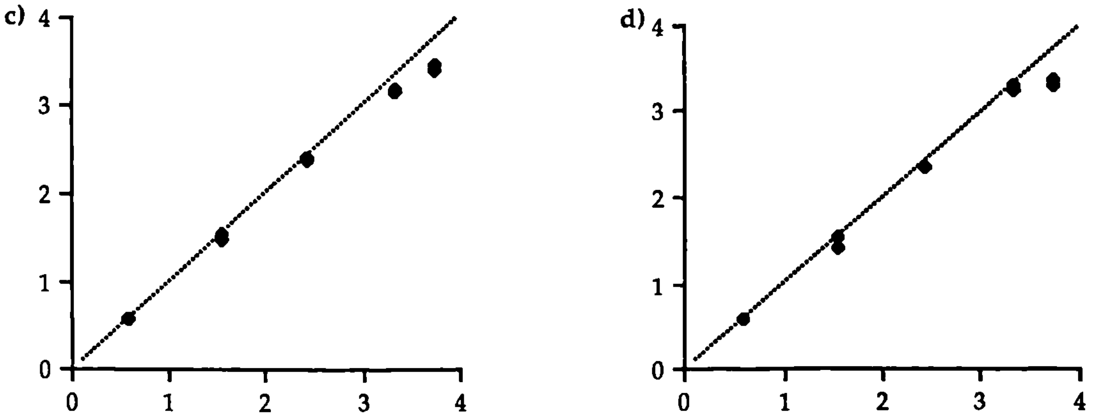
Monoculture

B. interruptus sowing density = 4 seeds m^{-2}



B. interruptus sowing density = 35 seeds m^{-2}

B. interruptus sowing density = 275 seeds m^{-2}



B. interruptus sowing density = 2200 seeds m^{-2}

B. interruptus sowing density = 5500 seeds m^{-2}

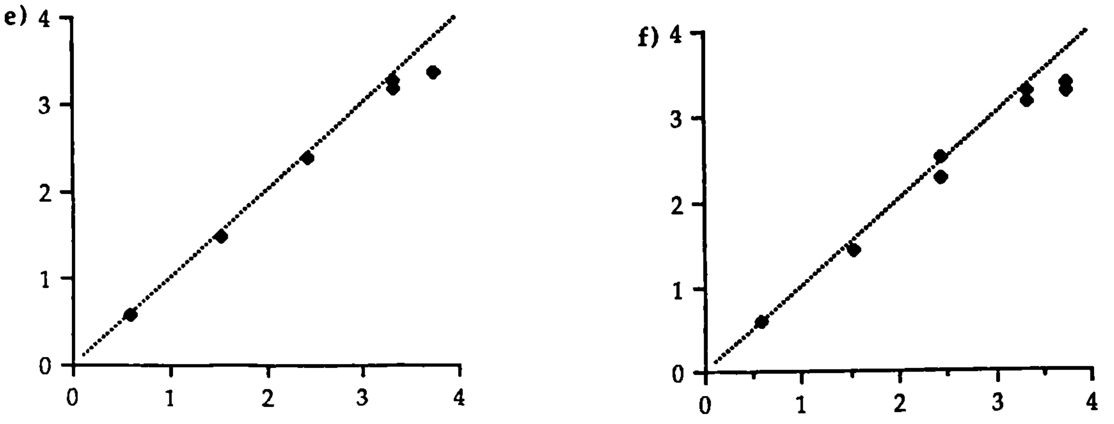


Figure 3.3.4
The effect of sowing density of *B. sterilis* on the biomass/plant of *B. interruptus*, each *B. sterilis* sowing density plotted as a separate line.

Note : no plants survived to harvest for the lowest *B. interruptus* sowing density (4 seeds m^{-2}) at the highest two sowing densities of *B. sterilis* (2200 and 5500 m^{-2}), nor for the second lowest *B. interruptus* sowing density (35 m^{-2}) at the highest sowing densities of *B. sterilis*. (5500 m^{-2})

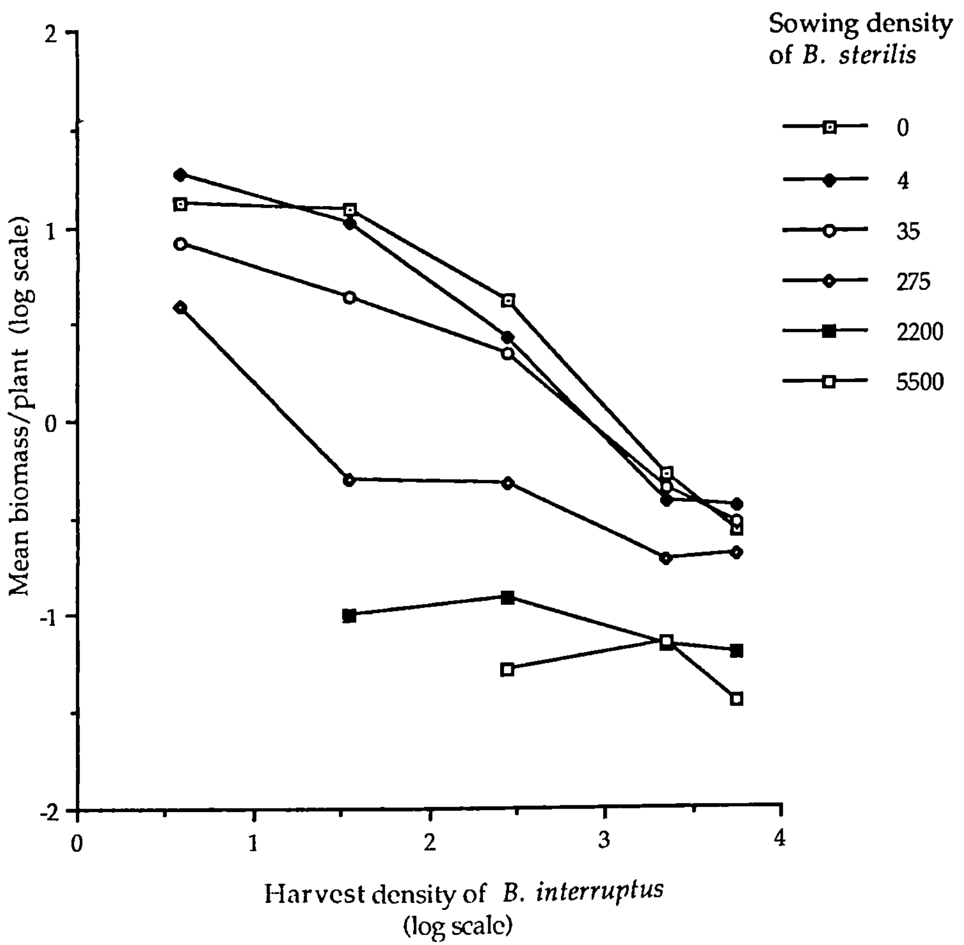
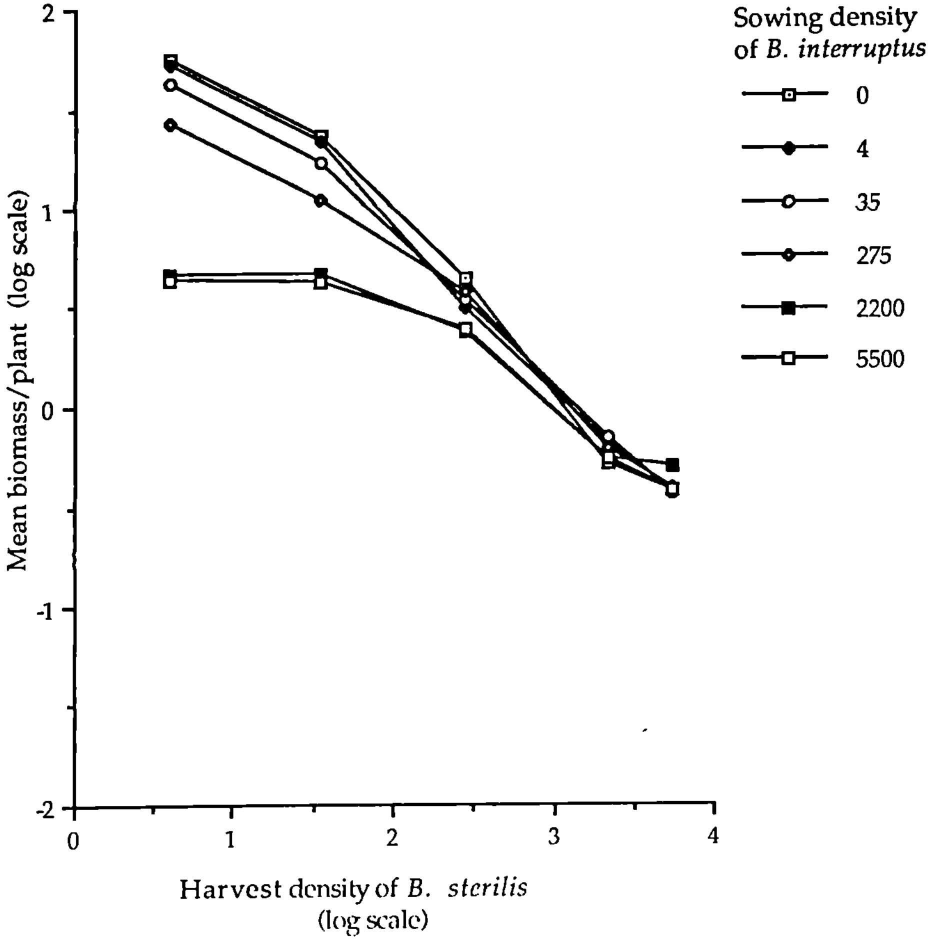


Figure 3.3.5
The effect of sowing density of *B. interruptus* on the biomass/plant of *B. sterilis*, each *B. interruptus* sowing density plotted as a separate line.



The estimates for the parameter **Biomass$_m$** for *B. interruptus* and *B. sterilis* were 23.82 and 73.71 g respectively (Table 3.3.b) which showed that, on average, *B. sterilis* plants grown in isolation were approximately three times heavier than isolated plants of *B. interruptus*. This estimate was supported by field observations (pers. obs.). The estimates of parameter **a** also differed by a factor of three, the value for *B. interruptus* being 0.0307 whereas for *B. sterilis* **a** was estimated as 0.0989. This difference in parameter **a** explains the response shown in monocultures (Figures 3.3.4 and 3.3.5) of reduced biomass/plant which occurred at a lower density for *B. sterilis* than for *B. interruptus*. As *B. sterilis* required greater space to achieve maximum weight, increases in density resulted in intraspecific competition at lower densities than experienced by *B. interruptus*. Estimates for parameter **b** were not significantly different from unity, 1.05 for *B. interruptus* and 0.95 for *B. sterilis*.

The equivalence coefficients for the two species were significantly different when compared using a *t* test ($P < 0.01$). *B. interruptus* perceived a *B. sterilis* plant as equivalent to 6.51 *B. interruptus* plants whereas *B. sterilis* perceived *B. interruptus* as equivalent to only 0.10 of a *B. sterilis* plant.

3.3.4 Discussion

Although density dependent mortality was detected by simple linear regression the density range over which this mortality occurred was insufficiently large to fit models describing density dependent mortality. A density range expanded to higher densities than those used here would be necessary, to include mortality that resulted in noticeable density dependent death of the plants at harvest, for more sowing densities, therefore providing sufficient data to fit models describing density dependent mortality.

3.3.4.1. Regulatory responses.

The responses to increased density by plant populations varies between species. For example, *Papaver* species showed mortal responses to increased density (Harper & McNaughton, 1962) whereas *Agrostemma githago* showed plastic responses (Harper &

Gajic, 1961; Watkinson, 1980). Regulation of populations of *Avena fatua* and *A. barbata* has been shown to be primarily through plastic responses although mortal responses also occurred (Marshall & Jain, 1969). Watkinson (1981) documented the simple allometric relationship between the seed production of an individual plant and the plant shoot dry weight for *Agrostemma githago*. The number of seeds produced per plant was proportional to the shoot dry weight. This relationship held true for plants grown over a range of densities and in the presence of a crop. The concept of reproductive output as a function of plant size or age, for semelparous species, has been discussed further (Watkinson & White, 1986). If this relationship also applies to the brome species it becomes obvious that plastic regulation via fecundity would have occurred, in this experiment, had the plants been grown to maturity. Plastic regulation of fecundity was indeed noted to have occurred in the first experiment reported in this chapter. However, in this experiment it is also apparent that mortal responses occurred, at the high densities, for both species. *B. interruptus* showed a very obvious mortal response in the population mixtures at the two highest densities of *B. sterilis* where no plants at all survived to harvest in these situations.

As mentioned in section 3.3.4 the parameter **b** can be used as an index of resource exploitation. Parameter **b** can also be regarded as a measure of a species ability to compensate for changes in density (section 3.2.4.2). The results from this experiment indicate that both species show exact compensation.

Using **b** as an index of resource exploitation values of **b** in excess of unity indicate less efficient resource capture at high density compared to low density. However, an apparent decrease in efficiency of resource capture may, in part, be due to changes in resource allocation at higher densities. For example, if allocation of resources to greater root production occurred there may be a decrease in the estimated value of **b** due to measurement of above ground biomass only whilst the actual resource capture remained constant. The lower value of **b** for *B. sterilis* may indicate that it was better able to compensate for the increased effects of competition at higher densities (Firbank & Watkinson, 1985). Differences or changes in growth form at higher densities that enable more efficient exploitation of the resources of nutrients, water or light might explain the better compensation of *B. sterilis,* for example a more erect growth form would facilitate light capture at high density.

3.3.4.2 Competition coefficients.

Gray (1981) investigated the competitive interactions of *B. sterilis* with cereals using replacement series experiments. For analysis he followed an extension of the original de Wit (1960) model by Bauemer & de Wit (1968). Predictions of a species yield in two species mixtures, at any density, were made from their yield responses to density when grown in monoculture. Although he derived equivalence values based on different calculations, following Bauemer & de Wit (1968), to the ones used here, the overall conclusions are pertinent. It was reported that the relative competitive abilities of the different species, spring barley, winter wheat and *B. sterilis,* changed over time depending on the periods of maximal growth of each species. Initially, *B. sterilis* was a weaker competitor than either spring barley or winter wheat but this relationship reversed for the winter wheat when *B. sterilis* exhibited maximal growth rate. The mean equivalences over time gave an order of competitiveness as follows

Spring barley > *B. sterilis* > winter wheat, the difference between *B. sterilis* and winter wheat being small.

Gray (1981) also reported differences in competitive ability for various nutrients. *B. sterilis* was more competitive than wheat in the uptake of potassium but less competitive for nitrogen and phosphorus. The implication of these findings is that the results of a competition experiment could be influenced by which nutrient is the limiting factor.

The results of an experiment (Howard *et al.,* 1989) where equivalences were calculated from above ground biomass of plants of *B. interruptus* and *B. sterilis* in competition with winter wheat, grown in glasshouse conditions, contrast with those of Gray (1981). Equivalences were calculated using the Watkinson model for two species competition whereas Gray (1981) calculated equivalences following Bauemer & de Wit (1968). Although the parameter estimates calculated by such models are not independent of the other parameters involved, in the case of the Watkinson model W, a and b (section 3.1.4), the rank order of competitiveness could be expected to be the same. However, the authors reported that the *B. sterilis* was a weaker competitor than wheat. Wheat perceived *B. sterilis* as only equivalent to 0.42 of a wheat plant. An equivalence for *B. interruptus* in relation to wheat was also quoted. Wheat perceived *B. interruptus* as equivalent to only 0.15 of a wheat plant, which indicated that wheat perceived *B. interruptus* as a weaker competitor than *B. sterilis* thereby providing support for the general findings of the experiment reported here.

Assuming a simple allometric relationship between seed weight and biomass of a plant, this experiment suggests that *B. sterilis* will out compete *B. interruptus* due to higher fecundity of this species in mixtures. High density populations of *B. sterilis* would competitively exclude *B. interruptus* leading to the conclusion that the latter would decline to extinction, almost regardless of the initial density of the *B. interruptus* population. Such a conclusion is based, however, on the assumption that the two species germinate simultaneously.

The rapid germination of *B. interruptus* on the stubble surface, in comparison to *B. sterilis*, (section 2.5) may be influential in determining the outcome of competitive interactions in undisturbed field conditions. This relatively earlier establishment of *B. interruptus*, nearly 40 % had germinated within two weeks of sowing compared with less than 10 % of *B. sterilis*, may prevent the later emerging *B. sterilis* from dominating a mixture of these grasses. At low densities of *B. interruptus* relative to *B. sterilis*, early establishment may, at least, ensure survival of the *B. interruptus* component of a sward even if *B. sterilis* dominated the sward in terms of above ground biomass. Differences in germination rate, between the species, were reduced when the seeds were buried just below the soil surface which implies that any cultivation practice that disturbed the soil and buried the seeds at shallow depths (not more than 50 mm, section 2.4) would favour *B. sterilis* when in competition with *B. interruptus*.

Gray (1981) reported the effects of differences in sowing dates on competitive interactions between *B.sterilis* and winter wheat. His results supported those of Sagar

(1959) who worked with a difference of 21 days between sowings and showed that this period was sufficient to give a clear competitive advantage to the earlier sown species. King (1971) reported that for mixtures of *Festuca rubra* L. and *Lolium perenne* L., sown simultaneously, the mean yield of *L. perenne* was greater than *F. rubra,* at all nutrient levels. However, when *F. rubra* was sown four weeks in advance of L. *perenne* at the same densities and nutrient levels, it produced greater yields than *L. perenne.* Yields of *L. perenne,* in this treatment, were reduced relative to the yields from the simultaneous sowings. It has been suggested (Donald, 1958; King, 1971) that the dominance of one species was attributable, in part, to an ability to occupy space in both the soil and leaf canopy at an earlier stage than the competitor.

3.3.4.3 Criticism of the experimental design.

Competition experiments using plants grown in pots have been criticised for the fact that the roots have to share a confined amount of soil whereas in field situations the root growth would be unrestricted and niche partitioning may occur. Evidence of below ground niche separation in grasses has been shown to occur, for example, *Avena fatua* and *A. strigosa* showed niche separation by differing rooting depths (Ellern *et al.,* 1970).

Reduction in the effects of competition for light may also occur in pot experiments due to lateral illumination (Grime, 1966). Prevention of this lateral illumination would necessitate solid screen pot surrounds to reduce illumination to the vertical component only which would be a closer imitation of a crowded stand of plants and increase light competition (Donald, 1958; King,1971; Snaydon, 1971). However, such screening would produce its own practical problems in construction and management of the experiment.

Advantages of pot experiments include easier control over the homogeneity of the soil and also abiotic factors by the use of covered conditions, e.g glasshouses. Although pot size restricts the density range at the lowest end of the scale it is frequently easier to maintain high density stands in the more controlled conditions that pot experimentation permit.

For maximum statistical stringency only one species biomass should be measured per pot to avoid the dependence of one species yield on the other species (Law & Watkinson, 1987). This experiment is subject to this criticism. However, such a design would have necessitated a doubling of the number of pots used and rendered the experiment too large to handle within the time available.

Chapter 4

Dispersal

4. Dispersal

4.1 Introduction

The basic unit of dispersal, in grasses, is the caryopsis, a single seeded fruit (van der Pilj, 1982), hereafter referred to as a seed. The functions of a seed include perennation, multiplication and dispersal as well as the release of genetic variability (Harper *et al.*, 1970). The dispersal of reproductive propagules is a crucial life history event in species which have evolved in ephemeral or unpredictable habitats (Southwood, 1977). Moreover, dispersal is a temporal as well as spatial phenomenon. Dispersal in time may be achieved by several mechanisms such as prolonged dissemination, seed dormancy and longevity and has been shown to have adaptive significance (Cohen, 1966).

Spatial dispersal mechanisms fall into five categories determined by the dispersal agent. Anemonochory is dispersal by wind, hydrochory dispersal by water, zoochory dispersal by animal agents and avichory dispersal by birds. The final category, autochory, describes plants that actively disperse their seed by methods such as explosive seed pods (van der Pilj, 1982). Grasses, as a class, display polychory, using more than one mechanism (van der Pilj, 1982). Zoochory tends to result in patchy distributions of propagules (Fenner, 1985) as illustrated by the distribution of the Costa Rican shrub, *Andira inermis* (W. Wright) DC., which was determined by the feeding habits and roosting sites of the bats that dispersed its fruits (Janzen *et al.*, 1976). The dispersal curves produced by anemonochory depend on the size and shape of the seed, wind speed and turbulence as well as the density of surrounding vegetation (Fenner, 1985). Height of release of seed is also influential, greater heights allowing more time for lateral movement of falling seeds (Sheldon & Burrows, 1973).

4.1.1 The ecological advantages of dispersal.

As a fitness trait, dispersal, has been argued to confer "ecological advantage", i.e positive fitness, which may be categorised into three groups as "Escape", "Colonisation" and finally "Directed dispersal" (Howe & Smallwood, 1982). The "escape hypothesis" was first proposed by Janzen (1970) who claimed that the advantages of dispersal were the avoidance of intraspecific competition and the avoidance of predation or disease at high densities. The hypothesis states that seeds that are dispersed from the immediate vicinity of parents plants experience a greater chance of successful establishment compared with those that remain close to the parent. Since this hypothesis was proposed, examples have been noted that both support and refute its validity. The most supportive example is *Mirabilis hirsuta* (Pursh) MacM. (Platt, 1976) which escapes from density dependent predation by ants and jumping mice by being dispersed. However, Silander's (1978) study of a Costa Rican shrub, *Cassia biflora*, showed no reduction in the proportion of seeds killed by weevil attack at lowered densities of dispersed pods but an apparent advantage in clumping for pollination.

The "colonisation hypothesis" applies to species living in successional communities and temporally heterogenous environments. Dispersal is essential for the location of habitable sites in which the species has sufficient time to reproduce before being excluded by plants latter in the successional progression or changes in the environment. Plants occupying such temporary habitats commonly have small seeds with a high dispersal potential (Howe & Smallwood, 1982) e.g. *Epilobium angustifolium* L.

The final category, "directed dispersal", describes the process by which propagules are relocated to specific habitats by animals. The environments to which the seeds are taken provide benefits in terms of improved establishment success. Examples of directed dispersal include pinon pine nuts which are cached by birds (Vander Wall & Balda, 1977) and seeds of numerous forest herbs carried to rotten logs and tree falls by ants (Thompson, 1980). Cost-benefit studies indicate that the benefits of increased likelihood of establishment for a proportion of the seeds are paid for by the losses of seeds due to consumption by the dispersing predators.

4.1.2 Dispersal in an arable ecosystem.

The dispersal ability of a weed species within an arable habitat is important in relation to the potential for a weed infestation to spread within the habitat. The spatial and temporal pattern of dispersal of seeds in arable habitats will be a function of both natural seed dispersal mechanisms and the effects of the husbandry practices that occur between seed set and germination. The exact pattern itself will reflect the interactions of these two processes in relation to a species life cycle, particularly the time of seed shed and the specific cultivation regime experienced. The stages during which the potential for seed movement by husbandry practices exists include combine harvesting (assuming some proportion of the weed seed remains unshed at the time and is sufficiently tall to be harvested) (Horne, 1953) and also during seed bed preparation (assuming the seeds are dormant).

The presence of weeds in a crop affects the efficiency of harvesting by altering the ratio of matter other than grain (MOG) to grain (Elliot, 1980). A large quantity of weed material will necessitate a reduction in the combine speed in order to maintain threshing efficiency. Changes in threshing efficiency will result in changes in the numbers of seed removed from the field with the grain. Passage through a combine can also affect the physical condition of weed seeds due to damage in the threshing and cleaning processes (Currie & Peeper, 1988). The literature suggests that more work has been conducted on the damage of grain during harvesting (King & Riddolls, 1960, 1962; Arnold, 1963, 1964) than on weed seeds, due to the economic significance of the crop .

The vertical distribution of seeds within the soil profile will determine the nature of seed movement during seed bed preparation. Early work on grasslands (Chippendale & Milton, 1934; Milton, 1939) showed that the majority of seeds remained within the top 10 cm of the soil, though some smaller seeds may be washed further down the profile. This vertical distribution may be altered by agriculture and the burrowing activity of animals. Some weed species from disturbed habitats are known to possess self burial mechanisms, e.g. species from the genera *Hordeum, Triticum, Avena* and *Erodium* (Harper, 1977). In deep ploughed land the distribution will be completely altered with seeds from the top few centimetres being buried upto 23 cm below the surface. Seeds will also become incorporated within soil clods, which can influence germination biology. A decrease in both germination and emergence has been reported for seeds in large clods, when compared to loose soil (Terpstra, 1986).

The first two experiments reported in this chapter were designed to quantify the shape of naturally occurring dispersal curves of the four brome grasses. These experiments used the technique of allowing seed dispersal to proceed, then monitoring the positions of the seedlings after sufficient time had elapsed for germination to occur. This method included any post soil contact movement, as has been shown to occur in some grass species (Mortimer, 1974), but detected only the distribution of the fraction of the seed population that survived to become established seedlings.

The subsequent experiments reported here investigated the effects of husbandry practices on seed dispersal at the stages of seed bed preparation and harvest. The aims of these experiments were to quantify seed dispersal due to husbandry practices and compare the distances moved by seed, due to these influences, with natural dispersal distances.

4.2 Natural seed shadows

Two experiments were conducted to map the seed shadows resulting from natural dispersal mechanisms in the four brome grasses. In the first experiment dispersal patterns from a point source, a single plant, were investigated and in the second, dispersal patterns from a linear front were considered. The two experiments were conducted in a similar manner. The plants were allowed to flower and disperse their seeds naturally, then the positions of seedlings arising from dispersed seed were recorded in the following autumn and early winter.

4.2.1 Materials and Methods

Each experiment employed a split plot design in which plants were grown either in wheat or in isolation, each main plot being replicated in three blocks. Sub plots contained one replicate of each species. Plot dimensions were 3 x 3 m. In the first experiment, main plots containing wheat were sown in November 1987 with winter wheat, *Triticum aestivum* L. cv Avalon, at a rate of 188 kg ha^{-1}. The bromes were planted into the experimental plots on 10 and 11.3.88 using plants which had been raised outside, in pots, since the previous November. Three transplants were placed centrally in each plot and thinned to a single plant once successfully established.

Seed for the second experiment was sown in the field on 18.10.88. Four seeds were planted every 0.1 m along a 1.5 m line within each plot and thinned to a single plant at each location once seedlings were established.

Throughout the period of both experiments, the plots were maintained free of other weeds by hoeing and hand weeding.

Final monitoring of both experiments was conducted, following seed dispersal, having allowed time for germination of a significant fraction of the dispersed seeds. In the first experiment the source plants were removed after concentric circles had been marked on the soil, centred on the source position, using 0.1 m radial increments. Numbers of seedlings within each circle were recorded.

In monitoring the second experiment, quadrats (0.1 x 0.1 m) were placed at right angles to the plot line and scored for seedling density. This was repeated at two points choosen randomly within the central 1 m of the transect and monitoring continued, moving away from the line, until two successive quadrats had zero scores for brome seedlings.

4.2.2 Analysis

Data for the first experiment were transformed to unit area basis (0.01 m^2 to be comparable with the second experiment). In both experiments seedling counts per sampling station (annulus, quadrat) were standardised by conversion to percentage of the total recorded for each plot. Examination of the data from the unidirectional transects of the second experiment also suggested that the frequency of distance declined in a gaussian manner away from a maximum at the source. In consequence seed shadows were fitted with a normal distribution using the Maximum Likelihood Program (Ross, 1987). The density function fitted was as follows

$$f(x) = (1/s\sqrt{2\Pi}\ )\exp(-0.5\ ((x-m)/s)^2)$$

where **m** is the mean and **s** the standard deviation.

As there were no differences apparent amongst the blocks and to enable the density function to be fitted to transect data, data sets were synthesized by randomly pairing replicate transects, after sign reversal of data in one of the pair. After assignment, the data from individual replicates were pooled, then fitted.

Chi-square analysis was performed to test

a) the goodness of fit of individual data sets to the model,

b) whether the data sets possessed the same shape of distribution whatever parameter values were fitted, (homogeneity of samples, H)

c) whether common parameters could be assumed for all data sets, (identity of fitted parameters, I).

4.2.3 Results

4.2.3.1 Dispersal from single plants

The single plants grown in the absence of the crop were accidently destroyed and hence no data were collected.

In wheat all the species showed a tendency to disperse a substantial fraction of their seed at a distance from the parent plant. Differences in the dispersal patterns of the four species were apparent from the distribution curves (Figures 4.2.1.a - d). The dispersal pattern of seed from *B. commutatus* plants showed a large fraction, 30 %, of seed remaining close to the parent plant with a further 60 % within 0.5 m from the source. Only a small fraction, approximately 10 %, was dispersed beyond this distance. The modal class of *B. interruptus*, which represented 30 % of the total number of seeds recorded, was between 0.2 - 0.3 m from the source with a further, approximately 40 % of seeds, dispersed beyond this distance. The patterns of dispersal of seed of *B. mollis* and *B. sterilis* were similar, without the marked modal classes that were apparent for the other two species. The distributions of dispersed seed of both *B. mollis* and *B. sterilis* had two peaks. For both species the majority of seeds were dispersed at a distance from the parent plant.

The greatest dispersal of seed was shown by *B. mollis*, the furthest seed being recorded 1.15 m from the source plant. *B. interruptus* displayed the most restricted dispersal, the maximum distance of a seedling from the source plant being recorded as 0.75 m. The rank order for maximum distance of seed dispersal in the four species was *B. mollis* > *B. sterilis* > *B. commutatus* > *B. interruptus*

4.2.3.2 Dispersal from a line of plants.

The seed distribution patterns of all four species, grown in pure stands and in wheat, were Normal and the mean of the distribution was centred around zero, the position of the parent plants (Table 4.2.a) with two exceptions. These exceptions were *B. sterilis* when grown in pure stand, ($t = 3.12$, $P < 0.01$, d.f. = 23) and *B. mollis* grown in the crop. The significant departure from zero recorded in the latter case was influenced by the large contribution from the frequency class at 0.2 - 0.3 m.

Table 4.2.a Parameter estimates for the curves which describe the natural seed shadows of the four bromes from a line of plants either grown in pure stands or in winter wheat. Parameters estimates: M, the mean, S, the standard deviation (and the standard errors of these estimates).

* - Significantly different at $P < 0.05$.

	Parameter Estimates				**Goodness of fit**	
Species	**M**	**M Standard Error**	**S**	**S Standard Error**	X^2	d.f.=23
In pure stands						
B. commutatus	-0.02399	0.03530	0.35374	0.02505	11.37	
B. interruptus	-0.03741	0.02909	0.28835	0.02068	26.33	
B. mollis	0.02398	0.03817	0.37912	0.02718	19.78	
B. sterilis	0.12705	0.03970	0.39624	0.02815	6.19	

Analysis of Chi-squared

	X^2	d.f.	
Identity of fitted parameters, I	165.41	6	*
Homogeneity of samples, H	42.97	36	

In wheat						d.f.= 14
B. commutatus	-0.03540	0.02792	0.27767	0.02010	14.09	
B. interruptus	-0.01326	0.01892	0.18767	0.01354	16.26	
B. mollis	0.07623	0.01892	0.18650	0.01355	36.51	*
B. sterilis	0.02813	0.03309	0.31152	0.02279	26.63	*

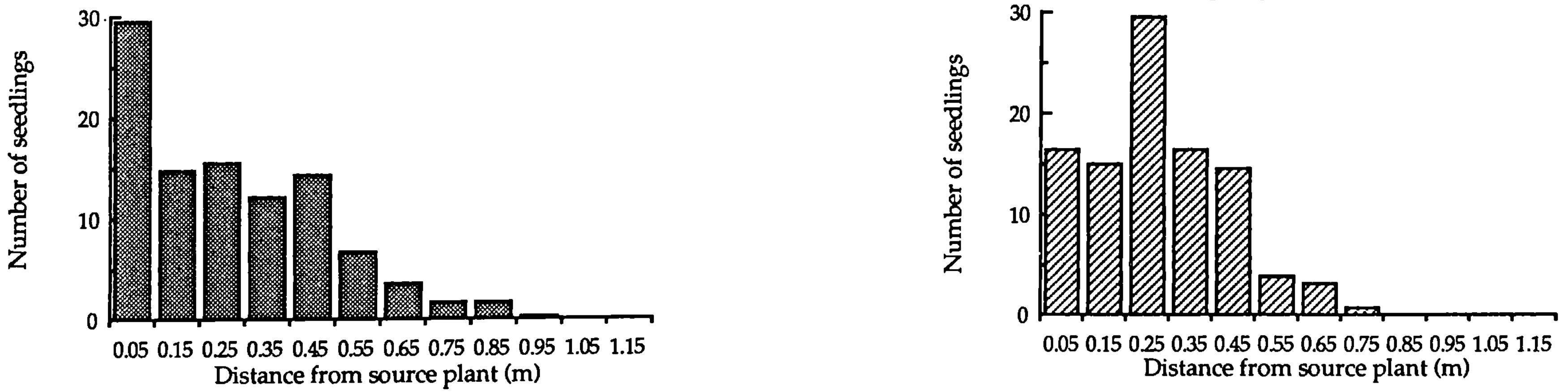
Analysis of Chi-squared

	X^2	d.f.	
Identity of fitted parameters, I	46.15	6	*
Homogeneity of samples, H	93.50	56	

Figure 4.2.1 Seed shadows from single plants, in wheat, for the four brome grasses.

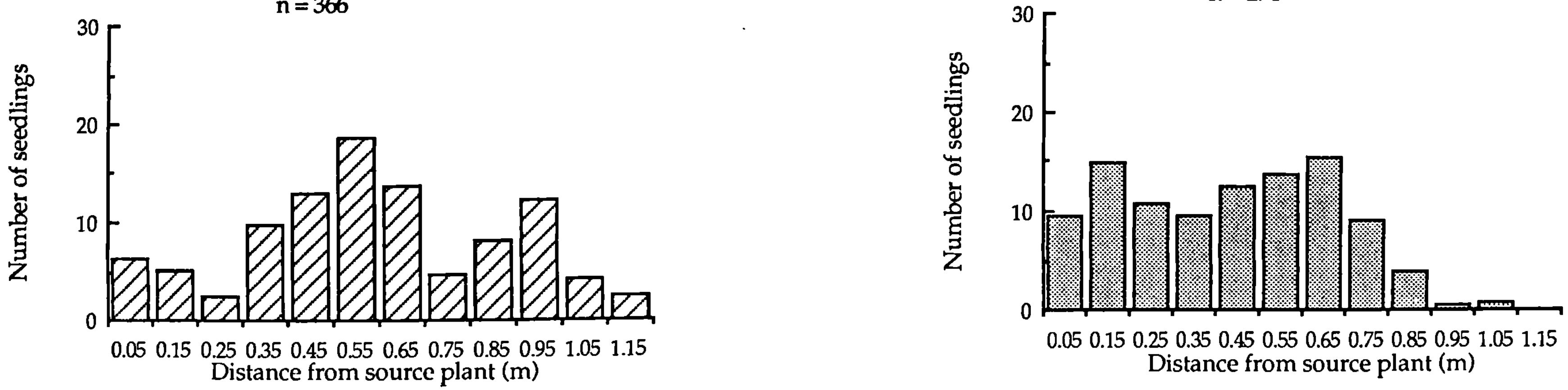
Number of seedlings (per 0.01 m^2) as the percentage of total recorded.

n = total number of seedlings recorded.



a) *B. commutatus* n = 366

b) *B. interruptus* n = 134



c) *B. mollis* n = 366

d) *B. sterilis* n = 271

Figure 4.2.2 Seed shadows from a line of plants, in pure stands, for the four brome grasses.

Number of seedlings (per 0.01 m^2) as the percentage of total recorded. Position of source plants indicated by arrow on horizontal axis.

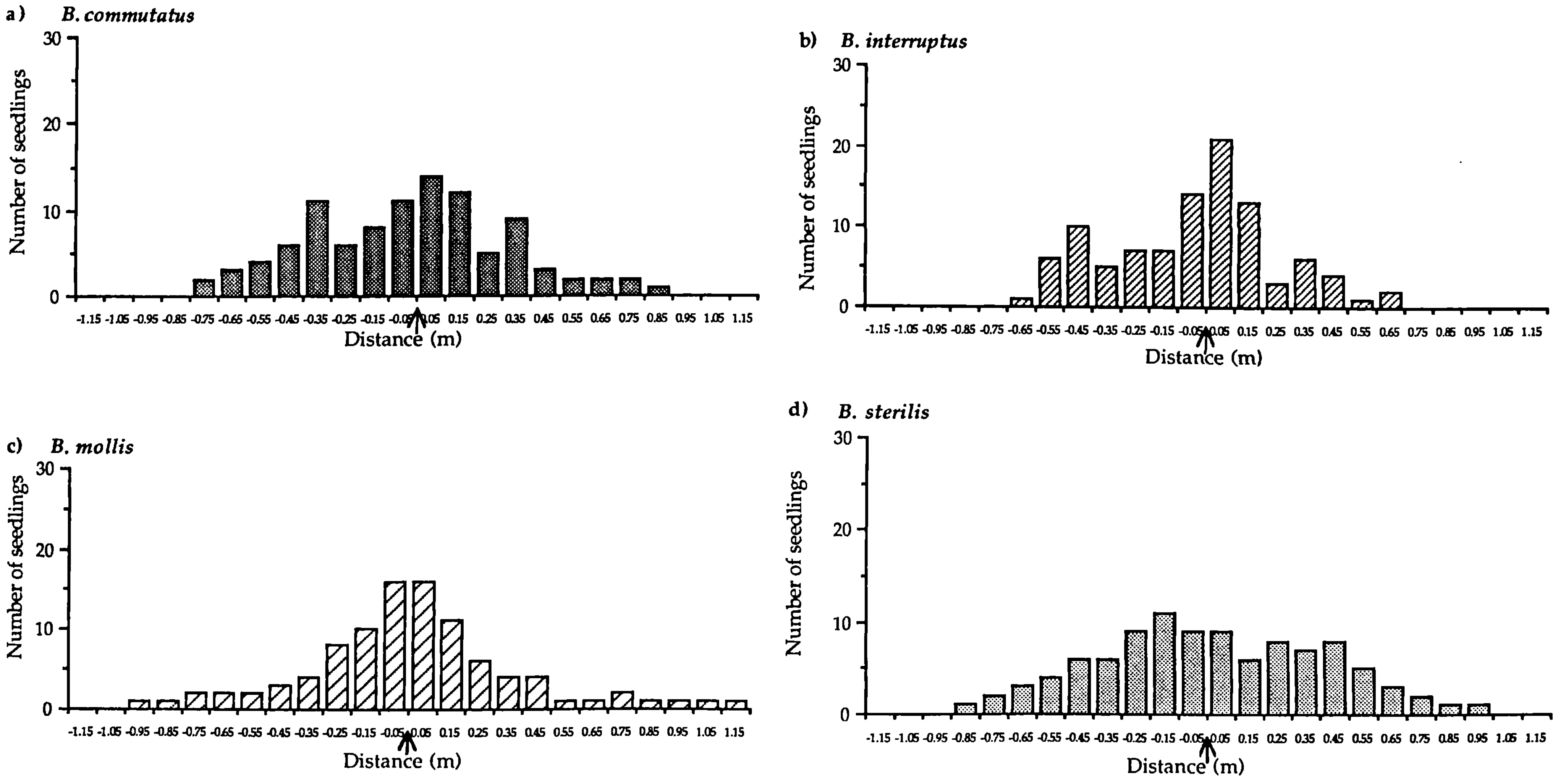
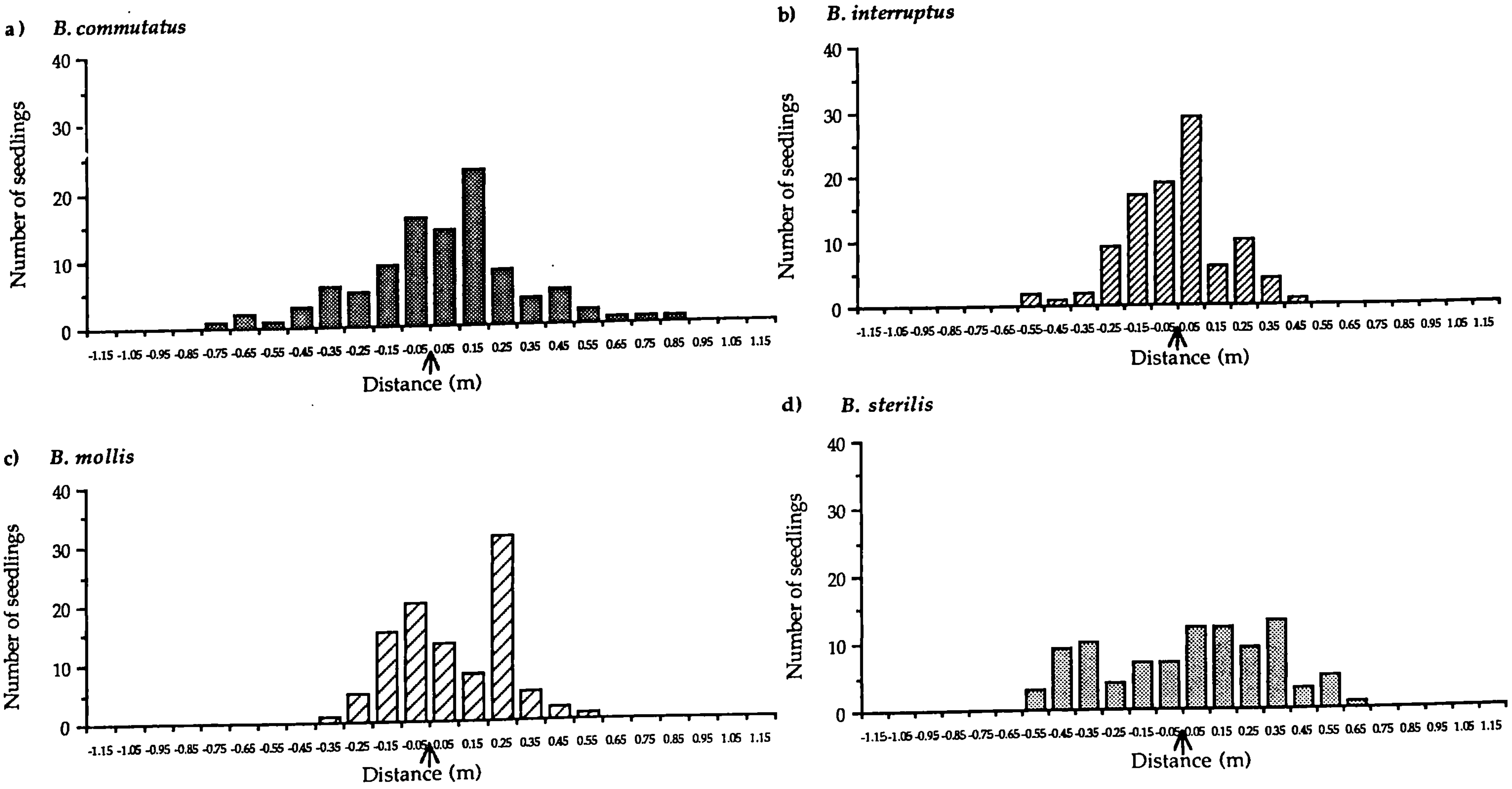


Figure 4.2.3 Seed shadows from a line of plants, in wheat, for the four brome grasses.

Number of seedlings (per 0.01 m^2) as the percentage of total recorded. Position of source plants indicated by arrow on horizontal axis.



There were significant differences between the distribution patterns of the four species in pure stands (Table 4.2.a). For the plants grown in pure stands *B. interruptus* had the smallest standard deviation, 0.29 m, which indicated that the seeds were dispersed over a narrower region than the other species. *B. mollis* and *B. sterilis* had similar, larger standard deviations, approximately 0.38 m. *B. mollis* had the maximum dispersal of the four species in the isolated conditions, the furthest seedlings were recorded 1.45 m from the parent plants (Figure 4.2.2).

The distribution patterns for the plants grown in wheat were also significantly different amongst the species (Table 4.2.a). Again the means were all close to zero showing that the bulk of the seed remained near the source plant. For all the species the standard deviations were lower than those for the distributions from isolated plants which indicated some reduction in dispersal. This effect was most obvious for *B. mollis* where the distribution appeared severely truncated. The standard deviations ranked in the same order as for the results for plants in pure stands with the exception of *B. mollis*. In this case *B. mollis* had the lowest standard deviation which indicated that dispersal had been severely restricted. The standard deviation for *B. interruptus* was similar to that for *B. mollis* , 0.188 m and 0.187 m respectively. As before the distribution of *B. sterilis* had the largest standard deviation.

The chi-squared analysis showed there was a significant lack of fit of a Normal distribution to the observed results for *B. mollis* and *B. sterilis*. In *B. mollis* this was largely accounted for by the exceptionally high count at 0.25 m . There was no statistically significant lack of fit in *B. commutatus* and *B. interruptus* fitted to a normal distribution.

4.2.4 Discussion

The dispersal of seed from single, isolated plants showed that all four grasses established a substantial fraction of the seedlings at a distance from the parent plant. Similar dispersal patterns for seeds have been reported for other grasses (Mortimer, 1974), *Papaver* spp. (Salisbury, 1942), the biennial herb *Verbascum thapus* L. (Salisbury, 1961) and *Eucalyptus regans* (Cremer, 1965). Close correlations between seed rain and numbers of seedlings established have been reported for the annual grass *Vulpia bromoides* (L.) S.F. Gray in a Californian coastal grassland but not for the perennials in the same study (Peart, 1989). For species such as these four bromes, with no persistent seed bank, the spatial pattern of recruitment will be highly influenced by the seed rain.

In general the distribution patterns for seedlings, from the line of plants, were similar to the observed dispersal patterns for seeds of other species from the edges of dense stands (Bakker, 1960; Cremer, 1965; Werner, 1975). The bulk of seeds remained close to the parent plants and seed density declined with distance from the parent.

Differences were apparent amongst the dispersal patterns of the four species. These differences were probably due to the differences in morphology of both the plants and their seeds. Cremer (1965) concluded that the distance of dispersal of seed by wind was influenced by the terminal velocity of the seed, the height of release and the air turbulence experienced during fall. Height of release was also cited as an important factor in determining the distance moved by seeds during dispersal by Sheldon and Burrows (1973). Morphological adaptations of the seeds affect the trajectories after release from the parent plant and the various adaptations possible have been discussed by van der Pilj (1982). Three of the four species used here have very similar seed shapes and weights (section 1.4), *B. sterilis* being the exception. However, the greatest differences in dispersal patterns were between *B. interruptus* and *B. mollis* which have similar seed dimensions. Differences in plant morphology may, however, explain them. In general, *B. mollis* plants tended to be taller than *B. interruptus* both in wheat and when grown in isolation (personal observation) which indicated that height was influential in dispersal. Height may influence dispersal as seeds, of similar weights, released from taller plants will have a longer period of fall during which lateral movement can occur. For plants in stands of vegetation this may be very important, more lateral movement being likely during fall above the canopy level, where turbulence would probably be greater. Another morphological difference between *B. interruptus* and the other three species, that is likely to have had an influence on the dispersal of seeds in the field, was the shape of the panicle (see Plate 1). Fracture of the culms of *B. interruptus*, before substantial dissemination of seed had occurred, was observed more frequently than for any other species. Germination of seeds whilst still retained within the compact panicles once in contact with the soil was also frequently observed, for *B. interruptus* , giving rise to dense clusters of seedlings.

The dispersal of seeds of all the species was shown to be reduced by a small extent, approximately 10 % of the maximum distance moved, by the presence of a crop when the maximum distances dispersed by each species was compared between within crop dispersal and dispersal from pure stands. This result was probably due to the interception of the trajectory of the seeds during fall by the surrounding vegetation. The similarity in maximum dispersal recorded between the single plants grown in wheat and the isolated line of plants may be due to the wheat crop in the first year, 1987/88, being sparce. This would present less of an obstruction to the dispersing seeds than a dense stand. In the second year the crop in which the line of plants grew, although planted at the same rate as the previous year, produced a denser stand. The differences in crop performance between the two years was due to waterlogging of the soil in the experimental area which occurred in the 1987/88 winter. The importance of surrounding vegetation on the dispersal success of grasses has been reported elsewhere (Rabinowitz & Rapp, 1981). The dispersal ability, measured as the lateral movement of the furthest 5 % of diaspores, was reduced by surrounding vegetation for seven prairie species.

4.2.4.1 Advantages of dispersal.

Of the three categories of ecological advantage discussed in section 4.1.1 the first two, "escape" and "colonisation", are most relevant to the bromes. The final category of "directed dispersal" can be discounted on the grounds that the majority of brome seeds are dispersed by wind rather than relocated by animal agents. Evidence for this comes from the shape of the dispersal curves which are typical of anemonochorous seed distributions. All four species would benefit from dispersal reducing the chances of density dependent mortality. Escape from disease and predation would also be advantageous but due to the morphology of the seeds, i.e. no fleshy fruit parts, avoidance of predation at concentrated centres is unlikely to be of major importance. Also considering the distances over which dispersal was recorded, in comparison to the foraging ranges of likely predators, i.e. birds and rodents e.g. field mice, the distances moved would be insufficient to ensure escape.

The major ecological advantage of dispersal for all four of the bromes is likely to arise from the fact that most populations exist in temporally heterogeneous habitats (section 1.2 & 1.5). Theoretical studies of animal populations have shown that populations living in unstable, heterogeneous habitats have improved persistence if dispersal occurs (Reddingius & den Boer, 1970; Roff, 1974a & b; Levin, 1976). Kuno (1981) illustrated theoretically that dispersal of individuals, even if random, had the potential to raise the average reproductive rate of the population as a whole. Kuno's assumptions have since been qualified (Metz *et al.*, 1983) but the general conclusion remained unchanged, that dispersal, of some fraction of the population, was beneficial in terms of persistence within a temporally variable environment. Although argued, theoretically, with reference to animal populations these conclusions are equally valid for dispersing plant populations as the terms used in the equations (per capita reproduction of dispersed and non dispersed populations, probability of dispersal) are equally appropriate to plants.

4.2.4.2 Experimental criticisms.

The experimental design used here relied on the assumption that the fraction of seeds surviving, and therefore recorded, at the time of monitoring was a random sample of the seeds dispersed from the plant. Part of this assumption is that the dispersal ability was not correlated with establishment success. Correlation would occur if, for example, heavier seed dispersed over shorter distances than lighter seed but had increased establishment success due to greater energy reserves. Reduction in the numbers recorded could also arise due to seedling mortalities prior to monitoring and again the assumption was that any such mortalities, if they occurred, were random and not density dependent. Alternative methods for measurement of dispersal cited in the literature included the use of markers, for example, radioisotopes (Colwell, 1953) and paints (Mortimer, 1974) or adhesive traps (Mortimer, 1974; Werner, 1975; Levin & Kerster, 1979; Rabinowitz, 1981).

The most common method used appeared to be adhesive traps but this method also only measures the location of a fraction of the dispersed seeds.

For the single plants, where numbers of seedlings were recorded per annulus (section 4.2.3.1), no indication of any directionality of dispersal could be achieved. Data could be collected per section of the annulii, if direction of dispersal was to be taken into consideration. However, for this study only the distribution pattern in relation to distance was required. The pairing of data sets (section 4.2.2) of the unidirectional transect data, to enable the statistical fitting of a Normal distribution function, produced a distribution curve in which no directional dispersal would be detected. This was due to the synthesis of these distribution curves from data collected along parallel transects from the central section of each line of plants. The effects of directional dispersal, if occurring, may have been detected had complete transects been recorded.

A significant lack of fit of a Normal distribution to the observed seed distribution curves for *B. mollis* and *B. sterilis*, in wheat, was indicated by the chi-squared analysis. In *B. mollis* this was largely accounted for by the exceptionally high count at 0.25 m and for *B. sterilis* by the platykurtic shape of the distribution. This significant lack of fit for two of the four species was probably due to the paucity of data, due to insufficient replication and difficulty locating seedlings within the lodged crop. This was the most plausible explanation especially in view of the fact that all four species had shown normal distribution patterns for the plants grown in isolation. Further replication would be expected to remove these effects.

4.3 Movement of seeds on the soil surface under soil cultivation.

Two experiments were conducted to investigate the movement of seeds on or just below the soil surface during seed bed preparation using different agricultural implements.

4.3.1 Materials and Methods

The first experiment, in the autumn of 1987, investigated the behaviour of two species reflecting two extremes of seed size namely broad beans, *Vicia faba* L. and oil seed rape, *Brassica napus* L. under three implements frequently used during seed bed preparation.

The implements used were;

1) Spring tine - a Kongskilde seed bed cultivator, triple k, which had four rows of fifteen tines. The tines were spaced approximately 120 mm apart on each row and the rows were staggered to produce tine tracks 60 mm apart. The tines were S-shaped, designed to allow vibration of the tine whilst maintaining a constant depth below the soil surface and had 6 mm wide points to prevent soil sliding up the tine and therefore, prevent vertical redistribution of the soil.

2) Seed drill - Fiona model D-78 used without any crop seed. This implement consisted of a single row of coulters, at approximately 100 mm intervals. The coulters were designed to dispense seed into small grooves created by discs situated in front of the coulters.

3) Rotovator - Roterra, a rotary power harrow with one row of paired vertical tines that rotated continuously. The rotating tines were followed by a row of fixed tines, the "clod comb" which held back large soil clods until they were broken down. Finally there was a spiral vee cylinder roller to ensure that a level seed bed was produced. In this experiment the implement was set with revolving tines at a depth of 60 mm and the roller at 30 mm above the surface.

The second experiment was performed in the autumn of 1988. In this experiment four species *B. interruptus*, *B. sterilis*, *Agrostemma githago* and *Brassica napus*, were used under two implements, the rotovator and spring tine. The bromes were choosen to provide contrast in seed shape and size (see section 1.4) and *A. githago* was included since the seed weight (approximately 8 mg) was intermediate between the two bromes and the seed was roughly spherical in shape. *B. napus* was included to allow a comparison between the two experiments.

The procedure followed in both the experiments involved sowing the seeds in a rectangular plot with dimensions of 0.25 x 1 m. The cultivation implement was drawn by tractor over this rectangle in a direction perpendicular to the longest side, on the same day that the seeds had been sown on the tilled soil surface. Monitoring involved counting the number of seedlings established in quadrats, (0.23 x 1 m in the first year and 0.25 x 1 m in the second), along a line transect in the plane of the passage of the implement. Monitoring was continued until no further seedlings were found in either direction from the starting location. The dates of sowing and monitoring for the first and second year were 30.10.87 and 5/6.12.87 and 3.11.88 and 15/16.12.88 respectively.

In the first year both species were replicated twice per implement in four blocks, totalling 24 plots, with the long axes of the sowing quadrats arranged in a single line. The direction of passage of the implement, whether from east to west or vica versa, was altered for pragmatic reasons i.e. to reduce vehicle turning required.

The second experiment was designed to include two types of cultivation and four species with all combinations replicated four times giving a total of 32 plots. The layout was arranged as three lines each containing one replicate and the first two an extra half replicate, to give four replicates in total.

4.3.2 Analysis

Inspection of the data revealed Normal distributions of seed movement with noticeable positive skewness and therefore all the data sets were fitted with lognormal frequency distributions using the Maximum Likelihood Program (Ross, 1987). A variable x has a lognormal distribution if log x has a normal distribution with mean μ and standard deviation σ. The probability density function of the lognormal distribution is described as

$$f(x) = (1 / x / 2\Pi\sigma) \quad e^{-((\log_e x) - \mu)^2 / 2\sigma^2} \quad , x > 0$$

where **x** is negative the distribution may be located by (**x** - **a**) where **a** describes the origin of the distribution. Two possible models may be fitted using this density function, either a two parameter or three parameter model. The two parameter lognormal distribution assumes that log(x) is normally distributed with mean μ and variance s^2. The three parameter lognormal distribution has the additional parameter **a**, the origin, such that log(x-a) is normally distributed. Implicitly the parameter **a** must be less than the smallest observation.

The two parameter model was used where there was no movement of seeds in the reverse direction of implement movement (i.e. backward) from the point of sowing. In such cases the origin of the distribution curve was fixed at zero. The three parameter model was used where backward movement of the seeds had occurred and hence the origin of the distribution curve was unknown. The choice of which model was appropriate to fit was made after visual examination of the data sets.

Initially each replicate of every treatment combination was fitted to the appropriate model, goodness of fit being assessed by chi-square (section 4.2.2). Replicate data sets were then automatically pooled and the models refitted.

Although, in all cases, statistically significant differences occurred between the parameter estimates for the individual replicates the basic shapes of the distributions were not significantly different (see Appendix 4, Table 1 & 2). In order to compare the different species under the same implement, the pooled data for each species was used in analysis to test for significant differences amongst species. Standard errors were calculated for all three parameters but it should be noted that due to the "severe skewness" of the distribution the standard error of the parameter **a** is of limited use in hypothesis testing (Ross, 1987).

4.3.3 Results

4.3.3.1 The 1987 experiment.

The spring tine, seed drill and rotovator implements resulted in different seed dispersal patterns (Figure 4.3.1.a - c). Seed of neither species moved backward, relative to the initial position, under the spring tine whereas under the rotovator seed of both species were recorded behind the point of sowing. Under passage of the seed drill, seed of *B. napus* showed reverse movement but the seed of *V. faba* did not. Therefore, the two parameter model was fitted to the *V. faba* data and the three parameter model to the *B. napus* data. The difference in their behaviour was sufficiently obvious as to remove the need for a statistical test.

The spring tine, Figure 4.3.1.a, caused the bulk of the seeds, of both species, to be displaced forward from the original position, upto a maximum of 2.19 m for *V. faba* and 1.73 m for *B. napus*. There was no reverse movement of seeds from the origin of the seed source relative to the direction of implement passage. The parameter estimates for the mean and standard deviation were not significantly different between the species (Chi-square = 4.14 , d.f. = 2, $P > 0.05$).

The seed drill, Figure 4.3.1.b, caused the least movement of seeds of all three implements. For *B. napus* the bulk of the seeds, 69 %, remained at the origin with 6 % displaced backward. The remaining 25 % were moved forward upto a maximum of 1.04 m. A very small fraction of the seeds were displaced upto 2.19 m forward. Seed of *V. faba* showed only forward movement, 50 % of the seeds remained at the origin and 42 %, in the second class of, upto 0.35 m. The maximum displacement was 0.81 m. Due to the absence of backward movement of seed of *V. faba*, data for the two species were fitted with different models and therefore no analysis was used to compare the two species.

The rotovator, Figure 4.3.1.c, caused a small fraction of seed of both species to be moved backward, 6 % of the *B. napus* seeds and 3 % of the *V. faba* seeds. Although, for both species, the largest fraction of seeds remained at the origin there was extensive forward movement. The largest displacement, for seed of *B. napus*, was 6.97 m whereas it was only 1.96 m for seed of *V. faba*. The parameter estimates for the two species showed significant differences in their values (Table 4.3.a). The origin, a, was estimated at 0.26 m behind the initial position for the *B. napus* but only 0.17 m behind for the *V. faba.*

4.3.3.2 The 1988 experiment.

Figures 4.3.2.a - d show that, as with the previous experiment, the distribution pattern of the seedlings was dictated by the implement (Rotovator or Spring tine) used. The individual implements produced the same basic distribution patterns as before. When the parameter estimates for the four species were compared there were significant differences amongst the species, under both implements, but not between the basic shapes of distribution curves (Table 4.3.b).

The differences amongst species were attributable to differences in the proportions of seeds moved both forward and backward. Under the passage of the rotovator *B. sterilis* showed the least backward movement, only 7 %, compared to 12 % for *B. interruptus* . The fraction of seeds that moved backward were 16 % and 17 % for the *A. githago* and *B. napus* respectively. The species also showed differences in the percentage of seeds which remained at the initial position. For *B. interruptus* 39 % of the seeds remained stationary whereas for *B. napus* this percentage was 56 %. The maximum distances moved by seeds of all the species were similar, in the range of 1.63 - 1.88 m. The maximum distance moved by a single seed of *B. sterilis* was 3.13 m and 2.63 m for *A. githago.*

Under the passage of the rotovator, the estimates of parameter **a**, the origin, increased consistently with decrease in seed size. *B. sterilis,* the largest seed, both by weight and shape, showed the lowest value of **a**, 0.21 m, where as *B. napus,* the smallest seed, showed the highest value, 0.32 m. This result was in agreement with those from the previous year where *B. napus* had produced a higher estimate for **a** than *V. faba.*

Under the spring tine treatment, there was no backward movement of seeds from the position of sowing for any of the species. Again chi-square analysis showed significant differences amongst the parameters estimated for individual species (Table 4.3.b) but not between the basic shapes of the distributions (Table 4.3.b). The means for each species were higher under the spring tine than the rotovator which indicated greater forward

Table 4.3.a Comparison of the Parameter Estimates for pooled data for Rape (*Brassica napus*) and Beans (*Vicia faba*) under three tillage implements. The parameters quoted are M, the natural logarithm of the mean, S, the natural logarithm of the standard deviation and where appropriate, a, the origin.

I - Identity of fitted parameters H - Homogeneity of samples

* - Significantly different at $P < 0.05$

Species		M	S	a	Analysis of Chi-squared			
Implement - Spring Tine						X^2	d.f.	
Brassica napus								
	Estimate	-0.84292	0.59778					
	Standard Error	0.06299	0.04832					
					I	4.14	2	
Vicia faba					H	21.54	14	
	Estimate	-0.86299	0.75301					
	Standard Error	0.07797	0.05997					
Implement - Seed Drill								
B. napus								
	Estimate	-1.32923	0.49825	-0.24560				
	Standard Error	0.18740	0.08646	0.04178				
V. faba								
	Estimate	-2.16082	0.74937					
	Standard Error	0.04672	0.04464					
Implement - Rotovator								
B. napus								
	Estimate	-0.67897	0.79246	-0.25790				
	Standard Error	0.17816	0.12570	0.06109				
					I	12.10	3	*
V. faba					H	7.93	20	
	Estimate	-1.29831	0.85917	-0.16990				
	Standard Error	0.18016	0.13754	0.02752				

Table 4.3.b Comparison of the Parameter Estimates for the pooled data sets of four species under the passage of a Rotovator and Spring Tine. The parameters quoted are M, the natural logarithm of the mean, S, the natural logarithm of the standard deviation and where appropriate, **a** , origin.

I - Identity of fitted parameters H - Homogeneity of samples

* - Significantly different at $P < 0.05$

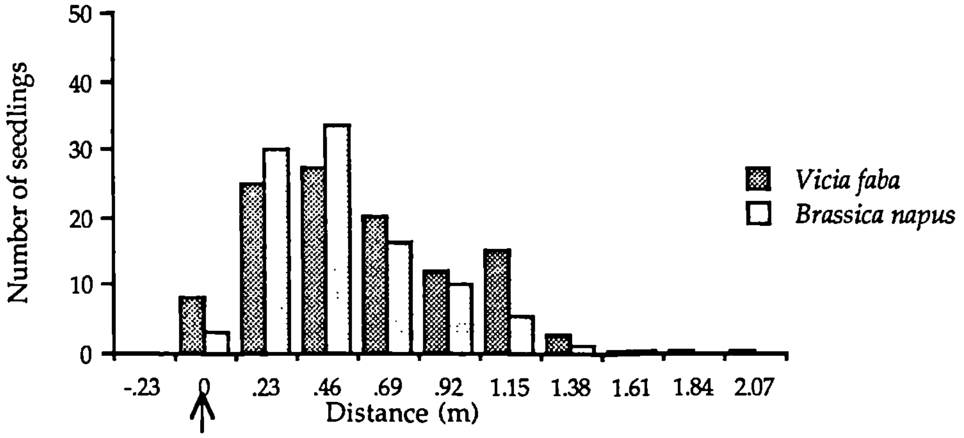
Species		**M**	**S**	**a**	**Analysis of Chi-squared**			
Implement - Spring Tine						X^2	d.f.	
B. sterilis								
	Estimate	-1.01138	0.71368					
	Standard Error	0.07553	0.05749					
B. interruptus								
	Estimate	-1.36680	0.72031					
	Standard Error	0.07797	0.05913		I	26.11	6	*
A. githago								
	Estimate	-1.53798	0.90210		H	26.01	24	
	Standard Error	0.09881	0.08311					
B. napus								
	Estimate	-1.42000	0.72421					
	Standard Error	0.07879	0.06183					
Implement - Rotovator								
B. sterilis								
	Estimate	-1.24226	0.85178	-0.21093				
	Standard Error	0.22648	0.16079	0.04177				
B. interruptus								
	Estimate	-0.96990	0.60504	-0.28619				
	Standard Error	0.24242	0.13406	0.07419	I	22.55	9	*
A. githago								
	Estimate	-1.17805	0.71230	-0.27730	H	7.26	28	
	Standard Error	0.30762	0.17568	0.07571				
B. napus								
	Estimate	-1.14159	0.48320	-0.32426				
	Standard Error	0.41578	0.17269	0.11830				

Figure 4.3.1 Movement of Beans (*Vicia faba*) and Rape (*Brassica napus*) due to the passage of three tillage implements. Data presented as the mean number of seedlings per quadrat (0.23 m^2) as a percentage of the total recorded.

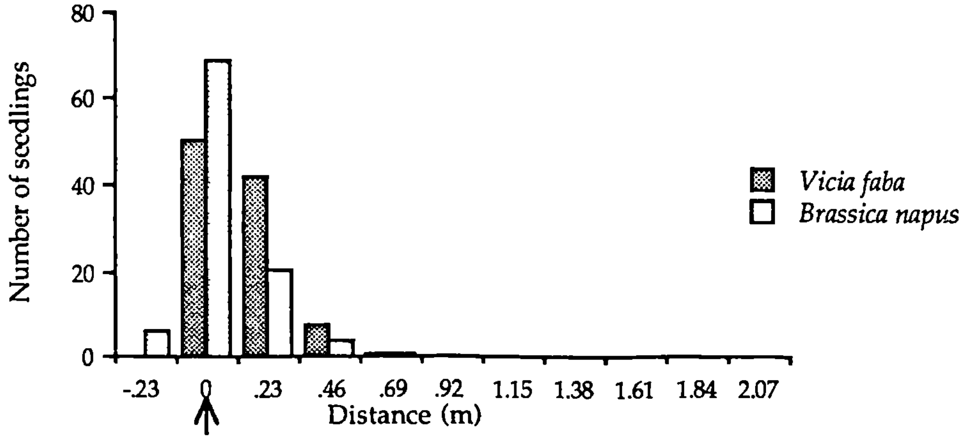
Initial position of seed marked by arrow on horizontal axes.

Note different scales on vertical axes.

a) Spring Tine



b) Seed Drill



c) Rotovator

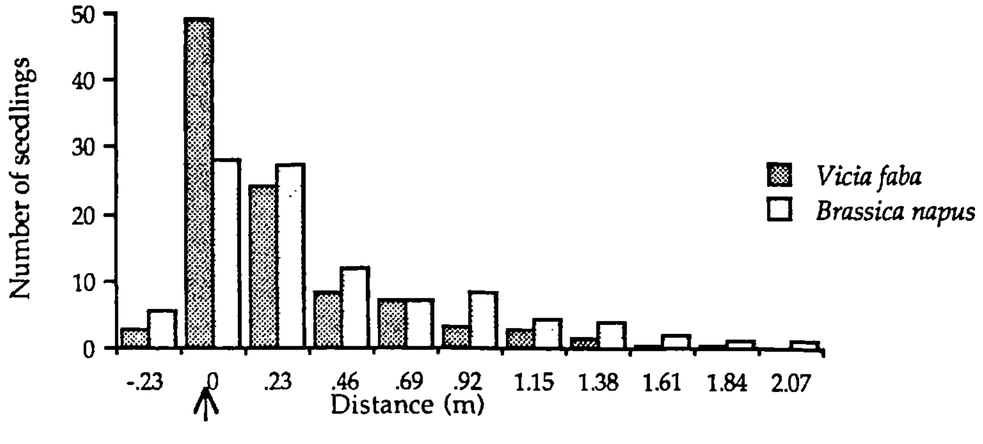
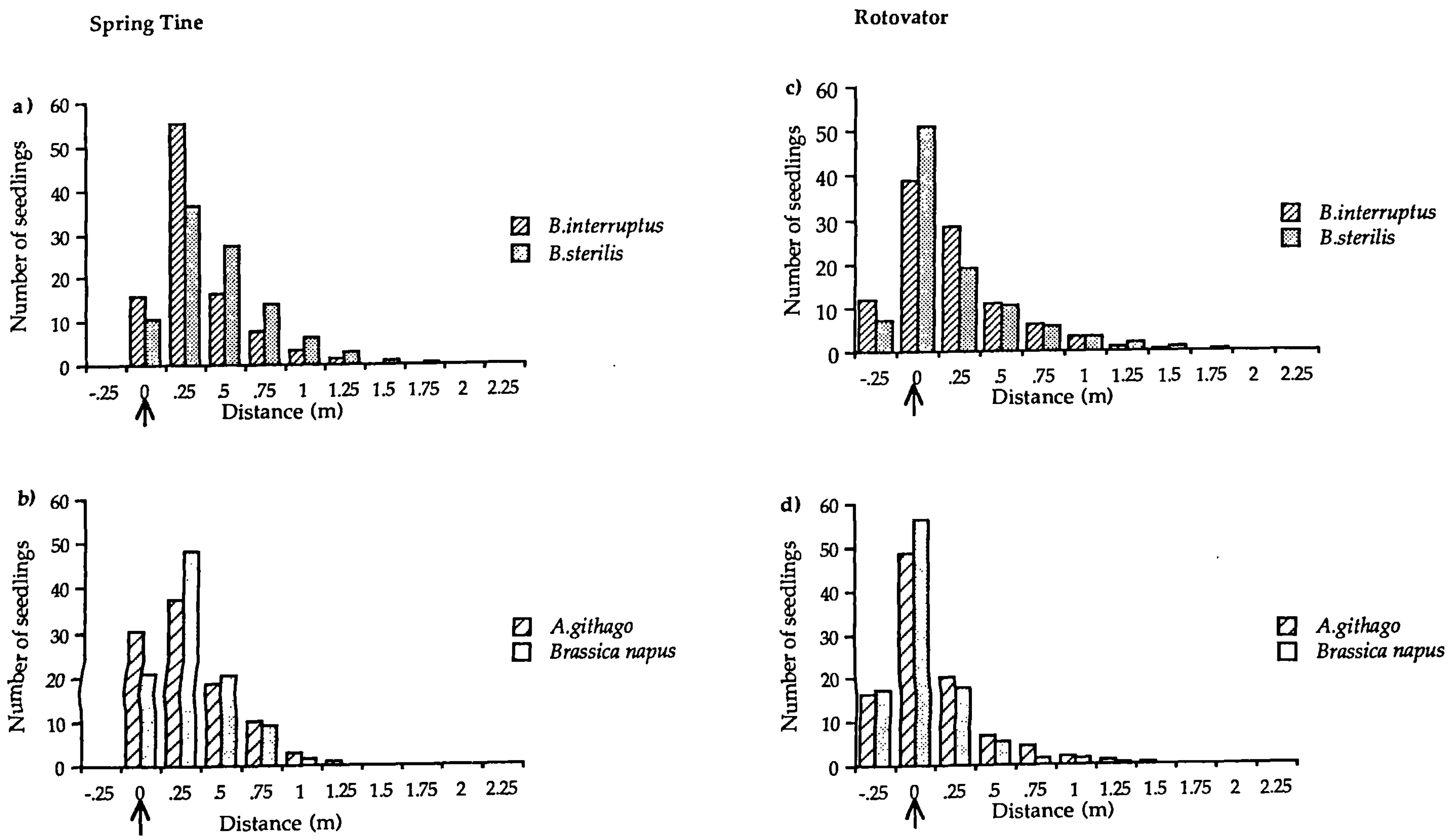


Figure 4.3.2 Movement of seed of four species, with contrasting seed shapes, due to the passage of a Spring Tine (a & b) and a Rotovator (c & d).

Data presented as mean number of seedlings per quadrat (0.25 m^{-2}). Initial position of seeds indicated by arrow on horizontal axis.



displacement of seeds. As before the actual percentages that remained at the initial position varied amongst the species. With the exception of *B. interruptus*, the percentage of seedlings found at the initial positions was lower under the spring tine than the rotovator.

4.3.3.3. Comparison of the results from both years.

B. napus was included in both experiments to provide a comparison of the movement of the seeds between the two years. Differences were apparent in the displacement of seeds caused by both the spring tine and the rotovator. Under the spring tine there was a higher percentage of the total number of seeds moved forward which resulted in a higher estimate for the mean. The maximum displacements also varied, the furthest movement in 1987 was 1.73 m compared to 1.13 m in 1988. Similar differences were also observed for the distribution pattern caused by the rotovator. The maximum displacement was reduced from 2.19 m in the first year to 1.63 m in the second year. The percentage of seeds that were moved from the initial position was different between the years also. 56 % remained stationary in 1988 compared to only 28 % in 1987. However, greater backward movement occurred in the second year, 17 % compared to 7 % in the first year, which accounts for the higher estimate of the parameter a produced from the 1988 data.

4.3.4 Discussion

Cultivators used in seed bed preparation have been shown, in these two experiments, to have a substantial effect on the distribution patterns of ungerminated seeds that were on or near the soil surface. The maximum distances moved by seed in the soil due to the passage of a cultivation implement were, in general, of a larger magnitude than the distances moved during natural dispersal. However, under all treatments, the majority of seeds remained within 2 m of the source position. The shape of the frequency distribution, which resulted from the passage of an implement, depended on the type of implement itself and, to a lesser extent, on the seed size. Each of the three implements used produced distinctive distribution patterns which proved to be consistent over the two years in which the experiments were conducted. This differentiation of patterns was due to the variations in structure and mode of action of the implements. The seed drill, which produced the least movement, consisted of a single row of coulters in contact with the soil whereas the spring tine was constructed to have four staggered rows of tines cutting the soil surface. The rotovator had a single row of paired tines but these rotated whilst in contact with the soil.

The fact that the patterns showed differences related to seed size indicated that the movement of seeds was not solely a product of bulk soil movement. If this displacement was solely due to bulk soil movement there would be no differences in distribution patterns between the seed sizes. The general trend observed was that the smaller seeds showed greater movement. The clearest example of this was in the estimates of parameter **a**, under the rotovator. The values increased consistently with decrease in seed size, in both experiments.

Both seed shape and weight may be influential in determining the distances moved. An analogy of the movement of seeds in soil can be made with the movement of clasts, coarse particles, in fluvial systems. Shape and size sorting is well documented in the coarse bedload of these systems and has been demonstrated to control the distances over which particles are transported (Bluck, 1982). Spherical seeds would roll more readily than seeds with flat surfaces. Awned seeds would probably require less force to roll in the direction perpendicular to the awn, than parallel to it and therefore the displacement of seeds may be influenced by the presence of awns. Seed shape and the presence of appendages on the seed, for example awns and hairs, may also influence seed movement by affecting the contact with soil aggregates. Small seeds would more readily be incorporated into soil aggregates, in cracks or within clods, and so be transported along with the soil. Hairs and awns may influence such linkage by reducing the proximity of seed and soil. Increased friction between moving seed and stationary surfaces may also result from the presence of hairs and awns.

The differences in behaviour of seed of the same species between the two years can be explained due to differences in the moisture content of the soil. Although no measurements were made at the time, the soil was noticeably wetter, in 1987, on the day that the implements were driven over the freshly sown seed. In the second year the soil appeared more friable, crumbling readily under the machinery and therefore being less inclined to move forward carrying the seed with it.

The vertical distribution of seeds in arable soils are largely determined by the depth of cultivation. Mould-board ploughing, where the soil is inverted to a depth of 23 cm, results in 43 % of seeds within the top 5 cm of the soil whereas chisel ploughing results in 60 % in the top 0.5 cm and no seeds below 10 cm (Mortimer, 1990). In an arable field, if unploughed, a high proportion of seeds, especially annuals recently shed, could be expected at or near the surface. In recent years the increased practice of minimum tillage, where the seed crop is sown directly into the stubble of the previous crop without deep ploughing, is likely to lead to an increase in the number of seeds subjected to lateral redistribution during seed bed preparation. However, this lateral redistribution would only be a significant effect for those species which have a substantial number of seeds that remain dormant until seed bed preparation. Seeds that have germinated and become established as seedlings are likely to be destroyed during seed bed preparation and hence population losses may occur during this phase of the life cycle.

4.4 Movement of weed seeds during combine harvesting.

The following experiment was designed to provide quantative data on the dispersal patterns of seeds of grass weeds when they pass through a combine harvester.

The experiment was conducted at Long Ashton Research Station, Long Ashton, Bristol between 17-19.7.89 when crop and machinery were available to allow the introduction of weed seeds into the combining process.

4.4.1 Materials and Methods

The experimental procedure involved the introduction of marked weed seeds into a combine harvester during normal combine harvesting of an arable grain crop. This marked material was deliberately inserted during forward combine movement at a point source and then collected, in both directions from the point source, after deposition from the combine.

A Claas Compact combine was used (Plate 4.1). This was a small commercial combine with a cutting width of 2.15 m which had been modified to allow a polythene sheet to be unrolled from the rear of the combine as the machine moved forward. Having a width of 1.22 m the sheet was sufficiently wide to collect all the chaff and straw deposited from the rear of the machine (Plate 4.2).

Trials were conducted in a winter barley crop, sown in the autumn of 1988 and ripe at the time of the experiment. The crop had an average tiller density of 653 tillers m^{-2}.

An initial combine run was conducted prior to which culms of the crop had been spray painted using commercial aerosol paints. The pattern of the deposition of coloured straw was observed in order to give some idea of the distances over which the combine was moving the bulk of the material. With this information, the experimental sampling strategy was devised. The experiment was designed to include three combine runs, each run involving the introduction of weed seed from different source material, in four replicate introductions per run. Seed was either supplied loose, being introduced manually into the combine, or on intact plants stood in the crop in the path of the combine.

Plate 4.1 The Claas Compact Combine

Plate 4.2 Chaff and straw collected on the polythene sheet.

Plate 4.3 Coloured *B. interruptus* plants placed in the crop prior to combine harvesting

Loose seed

Seventy gram lots of threshed, cleaned weed seed were individually sprayed with coloured paint prior to being introduced to the combine by dropping them, in mixture with barley grain, onto the cutter bar from above. During each run, four seed lots, differentiated by colours, were introduced, allowing 25 m to separate each point source of introduction. These points were identified, in advance, by canes placed at intervals along the length of the run.

Intact plants

Intact plants were stood within the crop forming a strip approximately 2.5 x 0.15 m, perpendicular to the direction of combining (Plate 4.3) at each of four 25 m intervals. Seed in the infructescence was colour coded at each source. Careful spraying ensured that seeds in the infructescence remained separate from one another. The mean number of seeds per panicle was calculated from a sample of 110 unthreshed panicles. This, together with counts of the number of panicles placed per strip enabled an estimate of the seed number entering the combine.

Seven hundred panicles, that had passed through the combine, were collected from the straw and the number of seeds remaining per panicle recorded.

During each combine run, volumetric grain samples (1 litre) were collected at 5 m intervals (positions marked by canes) from the threshed material entering the storage tank of the combine. This material was later weighed and the number of coloured seeds contained within the sample counted.

At the end of each run, deposited chaff was collected from the polythene sheet that had been laid out during combine movement. Initially excess straw was carefully shaken and removed by hand and pitchfork, then the polythene sheet was divided into either 1 m or 5 m strips and all the chaff collected. Five 1 m sampling strips were taken either side of the point of entry of the weed material and a further four 5 m strips taken in the forward direction of combine movement.

Chaff material was then sorted. Initially any remaining straw was removed and the individual chaff lots weighed. The chaff lots were then thoroughly mixed and a subsample (1/20 by weight) was taken from each lot. On average this subsample weighed approximately 10 g and 50 g for the 1 m and 5 m samples respectively. Chaff samples were then sorted by hand and the number of coloured seeds recorded.

Restricted crop and combine availability resulted in the opportunity for only four runs being taken. Weed material was allocated so as to give priority to the following contrasts: a) between seed sources (loose seed versus seed from intact plants), b) between species (primarily *B. interruptus* and *B. sterilis*) and c) between combine runs. Table 4.4.a shows the combinations of material used in each run. Loose seed of *B. commutatus* was used to represent a replicate of the loose seed of *B. interruptus* (due to a shortage of available seed) with the assumption that the seeds were sufficiently similar in size and weight to be considered identical. A fully crossed design, where all seed sources were included in all combine runs, was not used as it was anticipated that retrieval and differentiation of the coloured seed from the chaff would be difficult. At the design phase of the experiment it was unknown whether the seeds would be damaged or dirtied during passage through the combine, nor how visible the seeds would be within the chaff. A design was, therefore, used that, where possible, paired the seed sources to provide maximum differences in shape and colour of the seed with the aim of facilitating eventual retrieval of the seeds. Table 4.4.a also shows average combine speeds.

Table 4.4.a The pairing arrangement of seed sources across runs. Sources were replicated four times per run.

Run	**Source material**		**Average combine speed (km hr^{-1})**
1	Spray painted crop culms		1.80
2	*B. sterilis* *B. commutatus*	loose seed loose seed	*
3	*B. interruptus* *B. interruptus*	plants loose seed	1.82
4	*B. interruptus* *B. sterilis*	plants loose seed	1.64

4.4.2 Analysis

4.4.2.1 Fates of introduced seeds.

The proportions of introduced seed recovered in the chaff and barley samples were calculated. The percentages of the total number of seeds input into the combine that were retrieved from the chaff samples were calculated as follows. The number of seeds of each colour recorded from each subsample were summed, then multiplied by 20 to correct for subsampling. The values of the total number retrieved were then divided by the number input for each seed source. For the loose seeds the number input was calculated from the weight of the input sample, before the seeds were painted, i.e. 70 g, and the 1000 seed weights (section 1.4). For the whole plant seed sources the number of seeds input was calculated by multiplication of the number of heads harvested by the average number of seeds per head. The percentages of the numbers retrieved were, therefore, only approximations.

The percentages of the total number of seeds input that were retrieved from the barley samples were calculated from the summed number of each colour retrieved, multiplied by a correction factor to compensate for sample size. This correction factor was calculated knowing the crop yield m^{-2}, the distance between samples (5 m) and the mean sample weight (grain samples collected represented, on average, 18 % of the grain harvested over 5 m of forward movement). The corrected figure was then converted to a percentage of the total number of seeds, of each colour, that had been input into the combine. The input numbers, calculated as before, were used. Again only approximations of the percentages retrieved could be obtained.

Variation within and between runs

The experimental design precluded the comparison of variation in seed return amongst runs across all seed sources. Therefore variability amongst replicate seed introductions was analysed for individual seed sources in pairs of combine runs. Replicate data sets were standardised relative to the size of introduced seed lots and analysis of variance used to partition variation due to differing combine runs (2), introduced seed lots (4, differentiated by colour) and sampling points.

4.4.2.2 The patterns of seed distribution

Initial inspection of the data indicated that there was significant displacement of the introduced seed and that this seed was distributed lognormally (see section 4.3.2). Consequently data sets were fitted statistically with log normal distribution curves using MLP (Ross, 1987). Prior to fitting, data were standardised to percentage of the total number of seed retrieved from the chaff samples from each run. Replicate data sets for each seed source were fitted individually and as a pooled set.

4.4.3 Results

4.4.3.1 Dispersal from intact plants.

The majority of panicles, 75 %, that had passed through the combine harvester and been deposited along with the straw had had all the seeds removed (Figure 4.4.1). Only 12 % had one seed remaining per panicle. The remaining 13 % of panicles that entered the combine had two or more seeds remaining on exit. These results demonstrate how effective the threshing machinery, inside the combine, was at stripping the weed seed from the panicles.

An average of 65 % of the total seed input from the intact plants was retrieved from the chaff samples for the two runs. The bulk of this seed had been displaced backward from the source relative to the direction of movement of the combine. Approximately 20 % of the total seed input was retrieved between 2 - 3 m behind the source position with a further 11 % retrieved between 3 - 4 m behind the source (Figure 4.4.2). The distribution of seeds had a long tail in the forward direction although this represented less than 20 % of the total seed input. Of this fraction approximately 1 % moved to between 4 - 5 m forward from the source and 0.5 % moved to between 25 - 20 m forward.

A small fraction of the total seed input, an average of 6.5 % for the two runs, was estimated to pass into the grain storage tank. This showed that the majority of the *B. interruptus* seed had passed through the combine to be deposited in the chaff.

4.4.3.2 Fates of seed entering the combine.

Differences were apparent in the proportions of seed retrieved from the chaff and the barley samples both between the loose seed introductions and the seed from intact plants and also within the loose seed introductions amongst the three different species (Table 4.4.b). A greater percentage of the seed input was retrieved in the chaff from seed introduced on intact plants (65 %) compared to the loose seed introductions (50 %). For the loose seed introductions the proportion of seed retrieved, as a percentage of the total input, from the chaff increased with decrease in seed size. For *B. sterilis* an average of 46 % of the total input was retrieved whereas for loose seed introductions of *B. interruptus*, the lightest seed (section 1.4), an average of 59 % was retrieved.

The proportions of coloured seed retrieved from the barley samples also showed differences between loose seed and intact plant sources and amongst the loose seed sources. An average of 18 % of the loose seed introduced to the combine was retrieved from the barley compared to only 6 % of the seed introduced on intact plants. In contrast to the proportions retrieved from the chaff for the loose seed introductions the percentage of seed input that was recovered within the barley increased with seed weight. Again quoting the extremes, 23 % of *B. sterilis* was retrieved from the barley compared to only 10 % of *B. interruptus*. The proportion of seeds that remained unaccounted for was roughly constant at approximately 30 % for all seed sources. It, therefore, appeared from these results that the cleaning mechanism within the combine was sensitive to differences in seed size and weight.

The combine was cleaned at various stages of the experiment and the number of seeds found within the cleanings from different sections were recorded (Table 4.4.c). A greater number of seeds were found at the front of the combine than the back. For the loose seed this may have been a product of experimental error when throwing the seed onto the cutter bar from above. Comparison of the number of *B. commutatus* and *B. interruptus* seed found on the front of the combine for Run 2 & 3 with Run 4 indicated that more seed was trapped in this position from the loose seed introductions than from the whole plants. Allowing for the difference in number of runs and the number of seed introductions by different modes during these runs there were greater numbers of seeds lodged on the combine when loose seed was introduced. Although the percentages of the numbers input, that these seeds represent were very small, less than 0.01 %, in terms of actual numbers they were appreciable.

The analysis of variance of the numbers of seeds recovered from the chaff samples (standardised for number input) showed that there were highly significant differences in the numbers of seeds retrieved at the different sampling locations, as expected (Table 4.4.d). This analysis also showed that there were no significant differences between the two runs of replicate seed introductions (colours) for each seed source, with the exception of *B. sterilis*. For *B. sterilis* there was a significant difference between colours ($P < 0.0235$) within runs but not between runs.

Differences had been shown to occur in the fractions of the total seed input that was retrieved in the chaff for the *B. commutatus*/*B. interruptus* loose seed introductions (Table 4.4.b), which indicated that the assumption made in the design of the experiment was incorrect. However, when the numbers of seeds retrieved from the individual chaff samples were corrected for differences in the numbers input between species, then analysed, there appeared to be no statistical difference between *B. commutatus* and *B. interruptus* loose seed. This indicated that the proportions (of the fraction retrieved) that were deposited at the different sampling locations were similar for the seed of the two species, even though the overall fraction of input retrieved differed. Therefore, these two seed sources were considered as replicates in the further stages of the analysis where distribution curves were fitted to the data which had been transformed to a percentage of the total number of seed retrieved, in the chaff, for each sampling location. These results indicated that although the fraction of seed deposited in the chaff was determined by the seed weight, the proportions of this fraction deposited at specific distances was similar for loose seed of both *B. commutatus* and *B. interruptus*.

4.4.3.3 Distribution patterns of the dispersed seed.

Replicate data sets for both combine runs, for each seed source, were fitted with lognormal curves, individually and also as pooled sets, as described earlier. There was a statistical lack of fit to the lognormal distribution in some cases. For *B. sterilis* data the program failed to statistically fit distribution curves for six of the eight replicates, for *B. commutatus/B. interruptus* loose seed four of the eight replicates fitted without significant departure between observed and predicted and for the *B. interruptus* data five statistical fits were achieved. Visual inspection of the residuals, the differences between observed and predicted values, showed that the largest residuals consistently occurred in three areas of the curve (Figure 4.4.3.a). These were the modal region of the distribution which was frequently underestimated, the sampling locations between 3 - 5 m forward where the observed data frequently showed a small second peak in seed numbers and finally the tail of the distribution curve which was also frequently underestimated. In comparison Figure 4.4.3.b shows the model fitted to an individual data set where there was no statistical lack of fit. Bearing in mind these criticisms the log normal distribution curves, as fitted by MLP, were used to provide a general description of the seed distributions.

Comparison of the distribution curves for the three seed sources

The estimates of parameter **a**, the origin of the distribution, were similar for all three seed sources at approximately -4.18 m (Table 4.4.e). This indicated that the maximum movement of the seeds backward from the point of entry was the same for the three seed sources and therefore independent of seed shape and weight and also was independent of the mode of introduction of the weed seed material.

The estimates of parameter M, the natural logarithm of the mean, differed according to the modes of introduction of the seed. The values of M for the loose seed sources

Table 4.4.b Summary of the fates of introduced seeds. The figures quoted are the mean number of seeds collected, for the four replicate seed sources per combine run, expressed as a percentage of the total number input, with the standard error of each mean.

Seed Source	**Seed collected from**		
	Chaff	**Barley**	**Unaccounted for**
Loose seed			
B. sterilis	45.75 ± 3.17	23.25 ± 2.74	27.77
B. commutatus	49.25 ± 2.45	16.83 ± 3.37	33.92
B. interruptus	59.23 ± 2.67	10.48 ± 1.58	30.92
Intact Plants			
B. interruptus	64.80 ± 3.30	6.46 ± 0.45	28.77

Table 4.4.c The number of coloured seeds found on the combine at various stages of the experiment.

Approximate number of seeds per introduction: *B. sterilis* 7200; *B. commutatus* 9500; *B. interruptus* (loose seed) 16000: *B. interruptus* (plants) 23000.

Run Number	**Position of cleanings from combine**	**Number of seeds**	
		B. sterilis	***B. commutatus / B. interruptus***
2	Top of cutter bar	94	176
3	Top of cutter bar	0	482
2 & 3	Rear conveyer	0	1
2& 3	Front	107	422
2 & 3	Back	1	40
4	Front	119	16

Table 4.4.d Analysis of variance for the different seed sources to partition variation due to the two different combine runs, the four replicate introductions of coloured seed and the sampling points. Expected mean squares quoted for *B. sterilis* also apply to the other two analyses.

***B. sterilis* - Loose seed**

Source	d.f.	M.S.	F	$P_{(Ho)}$	Expected MS
Sampling location (SL)	13	705.25	31.08	<0.001	$Var_E + 4\ Var_{SL.R} + 8Var_{SL}$
Run (R)	1	19.07	0.15	NS	$Var_E + 14Var_{C(R)} + 56Var_R$
SL x R	13	22.69	0.47	NS	$Var_E + 4Var_{SL.R}$
Colour (Run) C(R)	6	125.31	2.61	0.0235	$Var_E + 14Var_{C(R)}$
Error	78	48.06			Var_E
Total	111	125.97			

***B. commutatus /B. interruptus* - Loose seed**

Source	d.f.	M.S.	F	$P_{(Ho)}$
Sampling location (SL)	13	1650.87	32.46	<0.001
Run (R)	1	483.79	4.59	NS
SL x R	13	50.86	0.66	NS
Colour (Run) C(R)	6	105.45	1.36	NS
Error	78	77.55		
Total	111	263.86		

***B. interruptus* - Intact plants**

Source	d.f.	M.S.	F	$P_{(Ho)}$
Sampling location (SL)	13	6746.88	68.97	<0.001
Run (R)	1	204.55	1.08	NS
SL x R	13	97.83	0.92	NS
Colour (Run) C(R)	6	189.82	1.78	NS
Error	78	106.66		
Total	111	888.68		

Table 4.4.e The parameter estimates for the distribution curves of weed seeds as dispersed by the passage through a combine harvester. Parameters quoted are M, the natural logarithm of the mean, S, the natural logarithm of the standard deviation and a, the origin. Data sets fitted were the pooled results for the eight replicates of each seed source.

* - Significantly different at $P < 0.05$

Seed Source	**Parameter Estimate**			**Goodness of fit**	
	M	S	a	X^2	df=10
***B. sterilis* - loose seed**					
Estimate	1.29214	0.93426	-4.15774		
Standard Error	0.04220	0.03281	0.06553	95.48	*
Median	-0.52				
***B. commutatus / B. interruptus* - loose seed**					
Estimate	1.38620	0.88225	-4.20240		
Standard Error	0.04247	0.03250	0.08150	82.39	*
Median	-0.20				
***B. interruptus* - intact plants**					
Estimate	0.84412	0.92421	-4.15380		
Standard Error	0.04191	0.03285	0.04106	74.89	*
Median	-1.83				

Analysis of Chi - squared

	X2	d.f.	
Identity of fitted parameters, I	142.68	6	*
Homogeneity of samples, H	252.77	30	*

Figure 4.4.1 Number of seeds remaining per panicle after passage through the combine harvester for a sample of 700 *B. interruptus* panicles.

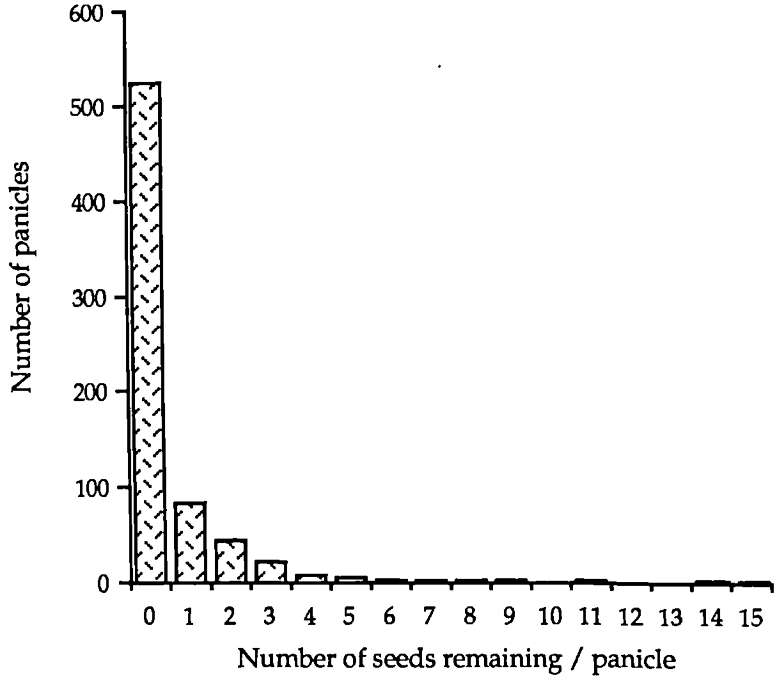


Figure 4.4.2 The dispersal of coloured weed seeds from intact *B. interruptus* plants , deposited in the chaff, due to passage through a combine during harvesting.

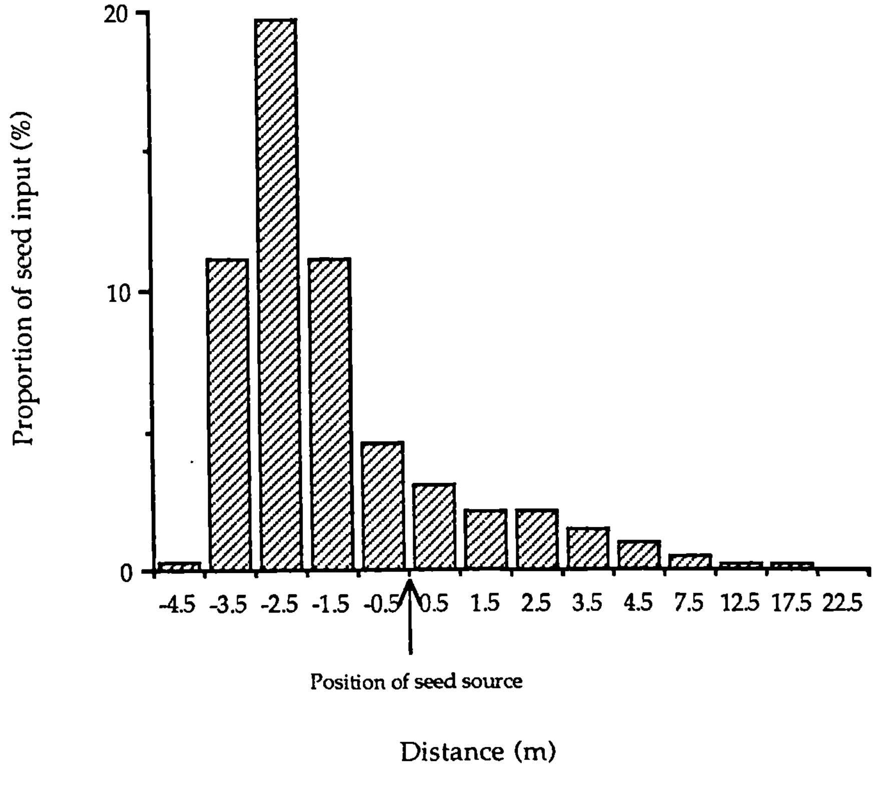


Figure 4.4.3 Fits of the function

$$y = 1 \; / \; ((x+a)\sqrt{2\pi}\,\sigma)\; e^{-(\log\,(x+a)-\mu))^{2}/2\sigma^{2}}$$

to two contrasting data sets from individual combine runs.

a) Source *Bromus interruptus* loose seed.

b) Source *Bromus commutatus* loose seed.

Note ordinates are scaled differently.

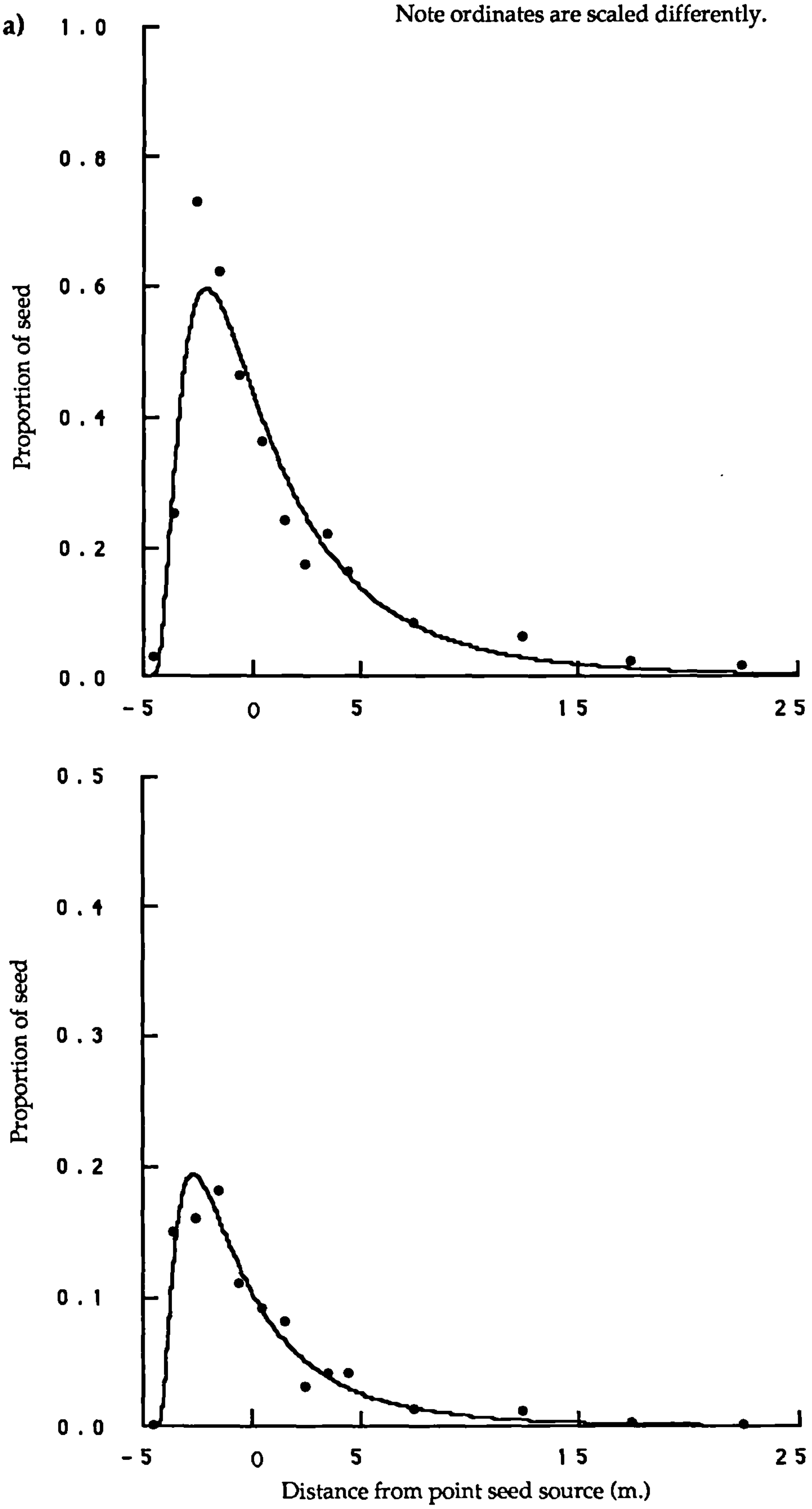
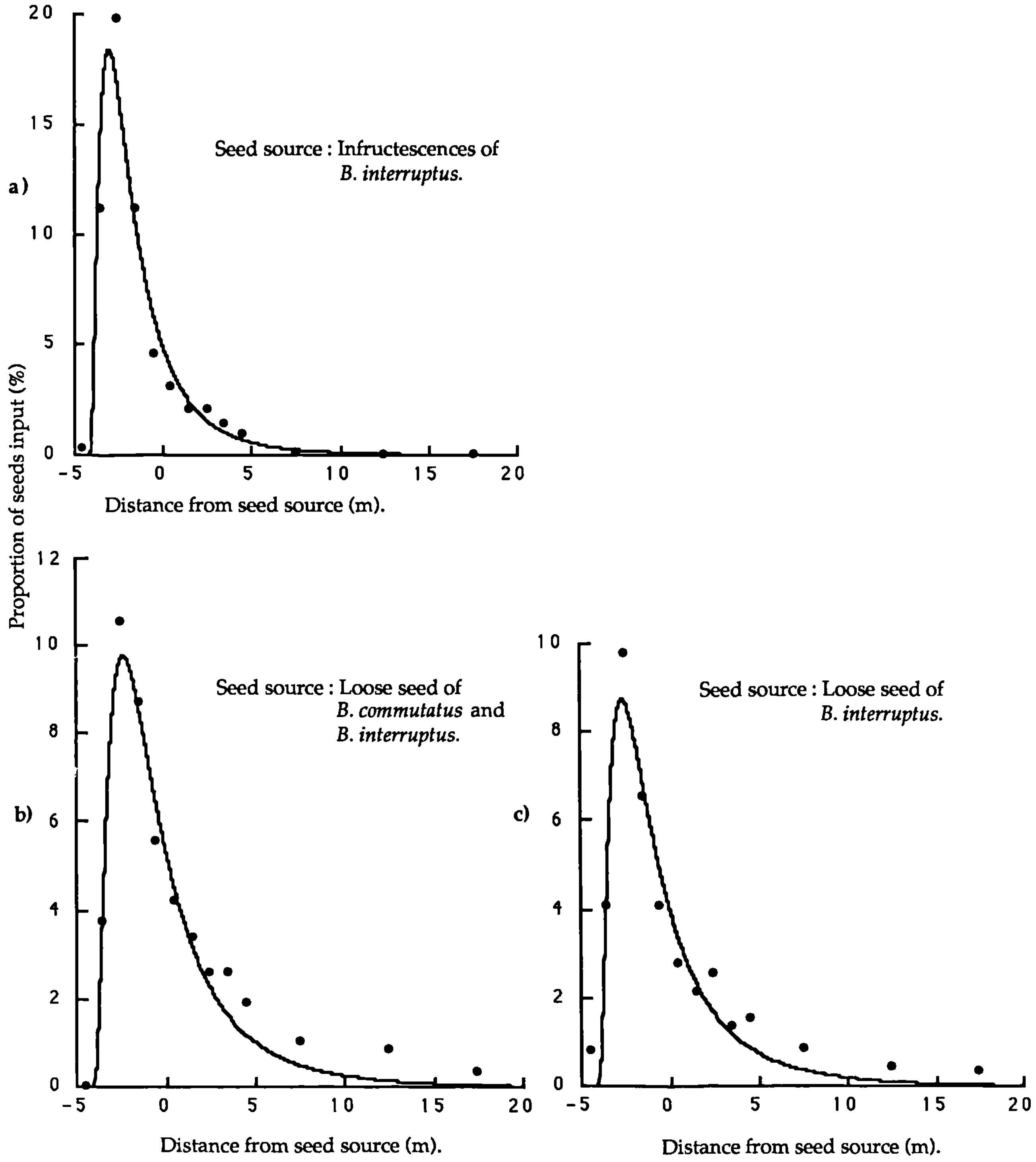


Figure 4.4.4 The dispersal patterns of seeds in chaff due to the passage through a combine harvester. Fitted curves are based on parameter estimates given in Table 4.4.e. Note ordinates are on differing scales.



were similar, 1.29 m for *B. sterilis* and 1.38 m for *B. commutatus/B. interruptus*. However, the estimate of M for intact plants of *B. interruptus* was lower at 0.84 m. This indicated that the mean was closer to the initial position for the seed from intact plants than for the loose seed.

Estimates of S, the natural logarithm of the standard deviation, were similar for all three seed sources. This indicated that the spread of the distributions were all similar as can be seen in Figures 4.4.4.a - c.

The median was also calculated for each distribution and again reflected the backward movement of a greater proportion of the seeds from intact plants compared to loose seed. Of the seed from intact plants 50 % was moved backward by 1.83 m or more whereas for the *B. sterilis* loose seed 50 % was moved beyond 0.52 m backward and for *B. commutatus/B. interruptus* loose seed this displacement was only 0.2 m behind the point of entry of weed material.

From Figure 4.4.4.a - c it can be seen that a greater fraction of the seed retrieved from the chaff of *B. interruptus* intact plants was displaced backward from the point of entry than for either *B. sterilis* or *B. commutatus/B. interruptus* loose seed. However, the proportions of loose seed retrieved of *B. sterilis* and *B. commutatus/B. interruptus* retrieved from the chaff in the forward tail of the distribution were greater than for the seed of *B. interruptus* intact plants.

The analysis of chi-squared showed significant differences ($P< 0.05$) for both the identity of the fitted parameters and the homogeneity of the samples. This indicated that common parameters were not applicable to the three distribution curves representing the three seed sources and that the shapes of the distribution curves varied amongst seed sources.

4.4.4 Discussion

The significant lack of fit chi-square values for the pooled data (Table 4.4.e) reflected the poor fits that were achieved for these data sets to lognormal curves. As with the individual replicates, the largest residuals occurred for the pooled data in three regions of the curves, the modal region, 3 - 5 m forward of the point of entry of weed material and in the tail of the distribution. Examination of the data for individual replicates and the pooled data sets indicated that the reasons for the poor fits in these three regions of the curves may have been due to;

1) Most of the observed distributions had a small second peak in the region of 3 - 4 m in the forward direction. This gave the impression of a second log normal distribution having been superimposed over the main distribution curve. This phenomenon could have arisen, in this situation, due to a threshing and cleaning procedure or a two stage cleaning mechanism within the combine. The majority of seeds would be removed at the first stage followed by a second smaller pulse of seed being deposited after the second cleaning stage.

2) The loose seed introductions consistently recorded greater seed numbers in the tail of the distribution than the intact plants. This elevated tail of the distribution could have occurred due to weed seed material caught on the front of the combine, for example on the cutter bar, falling from the machinery during forwards passage. Due to the method of introduction of the loose seed, i.e. being thrown onto the cutter bar, it would have been easy for weed seed material to lodge there temporarily. The data on the numbers of seed found on the combine (Table 4.4.c) after various runs showed that larger numbers of seeds were found on the front of the combine after runs where loose seed was thrown into the machine. This indicated that a greater fraction of the weed material from the loose seed sources became lodged in this manner, and therefore, may have been subject to loss from the combine as described above.

3) A final reason for the poor fits achieved by MLP for these distribution curves may have been a product of the size of the samples taken, especially in the modal region of the distribution curve. A smaller sample size would have provided more data which would have enabled a more accurate fit of the peak of the distribution. For classified data, where the frequency values of a continuous distribution are, for practical reasons, grouped into classes, parameter estimation, by MLP, depends to some extent, on the class limits choosen. In this case the class limits reflected the size of the samples. The precise effects of the choice of class limits depends on the number and size of samples (Ross, 1987).

4.4.4.1 The effects of combine harvesting on weed seed dispersal

From the results reported here it was apparent that the fate of seeds in the combine harvester was influenced by seed size. Comparison of the percentages of the loose seed sources retrieved from the barley and chaff samples indicated a larger percentage of the heavier seed, 23 %, entered the grain tank than the lighter seeds, 14 %. Conversely a higher percentage of lighter seeds, 54 %, were found in the chaff than the heavier seeds, 49 %. These differences were due to the cleaning of the grain inside the combine harvester via the sieves and rollers. The heavier, larger seeds were more likely to remain with the grain, rather than the smaller seeds, due to their similarity in size to the grain. A similar influence of seed size on the destination of seeds entering the combine has been noted elsewhere (H. Fogelfors & T. Fagerstrom pers. comm.). Seed entering the grain storage tanks, during harvesting, would be removed from the field along with the grain and therefore lost to the field population. The influence of seed size on the proportion of seed entering the storage tanks or being deposited within the chaff implies that larger seeded weeds would suffer the loss of a greater proportion of their seeds, from the field population, than smaller seeded weeds (assuming the same fraction of the annual seed production entered the combine).

A difference was also apparent in the destinations of seeds between the seeds of the same size but from different seed sources. The percentage of seeds from the whole plants found in the chaff, 65 %, was greater than for the loose seed, 54 %. Correspondingly there was a difference in the percentages retrieved from the barley samples, 7 % compared to 14 %, for the whole plants and loose seed respectively. These differences may relate to the fact that the whole plants would be threshed on entry to the combine and consequently pass through at a slower speed. The implication of this difference is that for future studies on the effects of combines on the dispersal of weed seeds it will be important to use whole plants whenever possible.

The magnitude of all the effects discussed above would depend on both the weed species under consideration, due to the influence of seed weight and on the specific combine used. Combines of different sizes could be expected to deposit the bulk of the chaff at a different position relative to the initial source position. Larger, longer combines, if moving forward at the same speed as a smaller machine, would probably deposit chaff material further from the source point. The precise design of the threshing and cleaning mechanisms may also effect the displacement of seed by influencing the speed at which material passed through the combine. The density of the weed infestation and moisture content of the cereal and weeds would also be influential in determining the patterns of dispersal due to the reduction in combine speed that dense or damp material for threshing necessitates (Elliott, 1980).

The most obvious influence of combine harvesting on the weed seeds was the increase in dispersal of the seeds compared to the distances moved during natural dispersal. In the experiment reported here combine harvesting was shown to disperse the weed seed such that the majority of the seeds were distributed laterally over 10 m, centred on the initial position. With the machine used in this study the peak of the distribution was 2 - 3 m behind the initial position but a proportion of the seeds was displaced forward. Small numbers of seeds, less than 1 %, were dispersed beyond 20 m forward of the initial position. Compared to the distances achieved by natural dispersal, a maximum 1.4 m recorded for *B. mollis* (section 4.2), the dispersal achieved by the combine harvester was very significant. The distribution produced by the combine had the effect of spreading the seeds over a greater area which would have implications for the fecundity of the plants that establish from these seeds, due to reduced intraspecific competition, and also for the migration of the population as a whole. The rapid spread of infestations of proso millet, *Panicum miliaceum* L., in maize fields in Canada have, in part, been attributed to dispersal of seeds by combine harvesters (McCanny & Cavers, 1988). Their work showed that just the dispersal of the small fraction of seeds remaining on plants at the time of harvest, over large distances, upto 50 m, had a pronounced effect on the weed population as a whole.

Studies on the dispersal of weed seeds during combine harvesting have been reported for crops other than wheat e.g. soybeans (Ballaré *et al.* , 1987) and maize (McCanny & Cavers, 1988). Both studies highlighted the increased dispersal of seeds that resulted from combine harvesting compared to natural dispersal. There have also been investigations reported concerning other effects of combining, for example, the damage to seeds sustained during passage through a combine (Currie & Peeper, 1988) and the changes in composition of the weed flora due to the collection of straw and chaff during the combining of Swedish cereal fields (H. Fogelfors & T. Fagerstrom pers. comm.).

The precise influence of combine harvesting, for any particular weed species, will also depend on the fraction of seeds retained on the plant at the time of harvest. Only this fraction will achieve the greater dispersal that results from passage through a combine and suffer the losses, due to removal of weed seed with the grain, that also occurs.

For the brome species, as discussed in section 2.8.4, *B. interruptus* which has the largest percentage , 45 %, of seeds retained in the panicle at the end of August, approximate time of harvest, will be most influenced by combine harvesting. Not only will a larger percentage of seeds enter the combine harvester but also more will be deposited along with the chaff than for the larger seeded *B. sterilis.* 35 % of *B. sterilis* seeds remained unshed by the end of August and thus would be harvested with the grain, the majority of this being deposited in the chaff whilst a considerable fraction would be removed with the grain. For *B. interruptus* 7 % of the numbers entering the combine would be expected to be lost to the field population due to exportation along with the grain. This results in 42 % of the total annual seed production being dispersed by the combine.

The use of combine harvesters also has the potential to spread weed infestations from one field to another or over a wider area (Horne, 1953; McCanny & Cavers, 1988). Weed seed can lodge in various places on the combine itself and thus be transported between fields if cleaning of the machine does not occur. In this experiment seeds were found resting in several places on the combine. Although they only represented a minute percentage of the numbers input, in actual terms they were sufficiently numerous to potentially act as an innoculum if dislodged in a previously uninfested field. Cleanings, that contained upto 7 lbs of grain, have been removed from combines after a whole field was harvested (George Cussans pers. comm.) which would inevitably contain some weed seeds also.

4.4.4.2 Possible fates of the unaccounted for seeds.

In the experiment reported here a large fraction, approximately 30 %, of the seeds input to the combine were unaccounted for after summing the numbers retrieved from the chaff and barley samples. There were three possible explanations for this disparity between the numbers retrieved and input, all of which were probably applicable to some extent. Firstly, as explained earlier (section 4.4.2) the percentages quoted were only approximations. Secondly, subsamples were taken, in view of the large volume and number of chaff and barley samples. Sampling errors could have arisen due to heterogeneity of the distribution of the coloured seeds within the chaff samples, despite mixing prior to sampling in an attempt to avoid this. The final source of seed loss was, again, a product of subsampling. Seeds at low density within the chaff or barley samples may not have been included within the subsamples taken. There was some evidence for this in that odd seeds were recorded, in a few subsamples, upto 100 m from the initial position. These presented such a small fraction of the total input that they were ignored in the analysis. Also if small numbers of seeds were carried long distances then they may have been dispersed beyond the area sampled and so have been unrecorded. Rarely has the analogy of "looking for a needle in a haystack" been more applicable than in regards to this experiment!

Chapter 5

General Discussion

5. General discussion.

5.1 Aim and approach of the research project.

The broad aim of the work reported in this thesis was to identify differences amongst the four brome species that could indicate an explanation for the variation in their abundances in Britain today. Use of these results in the construction of a management plan for the reintroduction *B. interruptus* is also considered.

The approach used involved comparative studies of selected aspects of the autecology of the four species, assessment of population growth of the four brome species in simulated headland conditions and an investigation of the distances of seed dispersal, both natural and as influenced by husbandry practices.

5.2 Summary of results and their implications.

Differences were apparent in the germination characteristics of the four bromes. All four species showed extensive germination, greater than 80 %, at the three temperatures used (12, 20 & 25 °C), with the exception of *B. commutatus* at 25 °C which had achieved only 70 % germination after 13 days (section 2.2). The rate of germination increased with temperature for *B. interruptus*, above 90 % germination being achieved after 4, 5 & 9 days at 25, 20 & 12 °C respectively. However, the other three species all showed a reduced rate of germination at 25 °C compared with 20 °C. Germination of all four species had occurred at 0 °C by monitoring on the 50 th day from the start of the experiment. Germination of these four species is unlikely to be limited by autumn temperatures in the U.K.

Differences between *B. interruptus* and the other three species were also marked when germination over a range of water availabilities was investigated (section 2.3). After 12 days greater than 85 % germination had been achieved by *B. interruptus* at all the water levels whereas the other three species showed reduction in the rate of germination with decrease in volume of water received per week. After 28 days the reduction in the cumulative number of seeds germinated at the lowest water level (1 ml/50g dry sand/week) compared to the higher rates (max. 35 ml/50g dry sand/week) was marked for all three species. Limited water availability may prolong the germination of *B. commutatus, B. mollis* and *B. sterilis*. *B. interruptus*, due to its rapid germination at low water availabilities, may be vulnerable to loss of the majority of seedlings if insufficient water is present for successful establishment.

None of the species were able to establish from seed buried at depths in excess of 100 mm (section 2.4). All showed establishment of the majority of seeds, greater than 90 %, from a depth of 10 mm. Differences were, however, apparent at the intermediate depth of 50 mm. *B. commutatus* and *B. sterilis* achieved approximately 55 % establishment from this depth whereas *B. interruptus* and *B. mollis* achieved only approximately 10 % establishment. These results indicate that mould-board ploughing, which inverts soil to a depth of 23 cm, would substantially reduce population numbers all four species.

The patterns of germination of the four species when sown on a field stubble surface or just beneath the surface of cultivated soil showed differences both between the treatments and amongst the species (section 2.5). When sown beneath the surface *B. sterilis* showed the most rapid germination, 65 % after 14 days. *B. interruptus* and *B. mollis* showed a similar temporal pattern of germination, both achieved roughly 40 % germination after 14 days whereas *B. commutatus* showed only 20 % germination by this time. All the species showed a reduction in the rate of germination when sown on the stubble surface compared to beneath the soil. However, this difference was most marked for *B. sterilis*, which is known to show light induced dormancy (Hilton, 1984), and the least apparent for *B. interruptus* , where at three of the four harvests the differences between treatments were not significant.

Under vehicle pressure none of the three species investigated, *B. commutatus, B. interruptus* and *B. sterilis*, showed increased mortality at either growth stage or treatment level used. Nor did *B. interruptus* show a reduction in seed yield (section 2.6). These results indicate that the bromes tolerated low intensity vehicle pressure in the conditions of this experiment and therefore, may tolerate low intensity vehicle pressure as would be experienced in a headland habitat.

Differences were shown amongst the species in the vernalisation/photoperiod requirements for initiation of flowering (section 2.7). The latest sowing dates from which seed was produced were as follows; *B. commutatus* - April, *B. interruptus* - April, *B. mollis* - February and *B. sterilis* - March.

The final autecological experiment investigated the rate of seed loss of the four species from spaced, single plants in monoculture and single plants grown in winter wheat (section 2.8). Again differences were apparent amongst the species and between the treatments. *B. interruptus* and *B. sterilis* displayed similar loss rates when grown in monoculture and in wheat, *B. sterilis* disseminated seed faster than *B. interruptus*. *B. commutatus* and *B. mollis* showed an increase in the rate of seed loss when grown in wheat compared to monoculture. Although dissemination of seed was slower for *B. commutatus* and *B. mollis* in monoculture, when grown in wheat the loss rates of both *B. commutatus* and *B. mollis* were greater than those of *B. interruptus* and *B. sterilis*. These results imply that the percentage of the annual seed production that enters the combine during the harvesting of the crop is different for the four species. A greater percentage of *B. interruptus* would enter, and therefore be dispersed by, the combine than for the other species.

Assessment of seed production in simulated headland conditions (section 3.2) showed that, although seed production was reduced when the grasses were grown in two densities of wheat compared to weed monocultures, all the species produced seed at all the sowing densities (0.5 - 10,000 seeds m^{-2}). All species should, therefore, persist in headland conditions, assuming no cultural or chemical control measures are applied. No density dependent mortality was recorded for the bromes over the range of sowing densities used in this experiment but regulation of population size by plastic changes in seed production per plant were evident for the four species.

The relative competitive abilities of *B. interruptus* and *B. sterilis* in mixture were assessed (section 3.3). *B. sterilis* appeared to outcompete *B. interruptus* in the experimental conditions employed. *B. sterilis* showed density dependent mortality at the two highest sowing densities (2200 and 5500 seeds m^{-2}) irrespective of the sowing density of

B. interruptus whereas increased mortality was evident for *B. interruptus* with increased sowing density of *B. sterilis*. These results imply that *B. sterilis* may outcompete introductions of *B. interruptus* in field conditions.

Investigation of the influence of husbandry practices on the dispersal of weed seed showed that these influences could have a very significant effect increasing the natural dispersal patterns of seed and that the effects were determined both by the agricultural implement and, to a lesser extent, seed size (Chapter 4). Passage of intact *B. interruptus* plants through a combine harvester was shown to disperse the seed over a 25 - 30 m range, the bulk of the seed being moved approximately 3 m backward from the source relative to the direction of combine movement with a long tail (25 m) to the distribution in the forward direction (section 4.4). Seed size was shown to influence the destination of seed entering the combine, a greater proportion of the larger *B. sterilis* seeds entered the grain tank than the smaller *B. interruptus* seeds. Passage of tillage implements over seeds on the soil surface was also shown to cause a greater dispersal of seeds when compared to the distances moved, approximately 1 m, achieved by naturally dispersing seed. Dispersal of the bulk of the seeds over a distance of 2 -3 m was recorded and smaller seed were detected to move further (section 4.3). The results from Chapter 4 showed that husbandry practices investigated greatly increased the dispersal of seed of the grasses compared to that achieved naturally.

5.3 Broader implications of these results.

5.3.1 Possible reasons for the extinction of *B. interruptus*

B. interruptus declined from peak abundance from the late 1920's and is now classified as extinct. The reasons for the disappearance of this species are probably complex but the results from this research provide some indication of factors that may have been influential. Experimental work has shown that this species is unable to establish from seed buried at depths greater than 50 mm. The use of tractors in British agriculture would have begun in the 1920's and become more widespread through the 1930's. This increased mechanisation of ploughing would probably have resulted in more thorough and possibly deeper inversion of the soil thereby preventing establishment of *B. interruptus*.

Lack of an aggressive competitive ability may have resulted in the exclusion of *B. interruptus* from field margins and hedge bottoms. The fact that the majority of seeds germinate rapidly in field conditions indicate that the species would be vulnerable to loss of whole populations and the limited natural dispersal and narrow geographic range (Perring & Walters, 1976) would minimise chances of reintroduction.

The demise of *B. interruptus* contrasts with the rise of *B. sterilis* from a widespread but inconsequential hedgerow and wasteland inhabitant to an increasingly problemmatic weed in cereal systems. This increase in abundance of *B. sterilis* has been attributed to the shift to minimum tillage in seed bed preparation of cereal fields (Anon, 1981). Deep ploughing is avoided and so *B. sterilis* seed remains sufficiently near the surface for the majority of seeds to establish, especially amongst autumn sown cereals. The increase in abundance of *B. sterilis* may well have been accelerated by dispersal of a small fraction of the annual seed production during combine harvesting. Although it is usually assumed that all *B. sterilis* seed is shed by the time of harvest an experiment reported in this thesis showed that 35 % remained unshed at the end of August. McCanny and Cavers (1988) demonstrated how the redistribution of only 2 % of the annual production of the weed proso millet during combine harvesting of maize crops had a dramatic effect causing the rapid spread of this weed. Experimental work on the dispersal of bromes via a combine harvester showed that the majority of seed entering the machine was returned to the field and distributed over a range much greater than that achieved naturally. Therefore the greater dispersal caused by combine harvesting may well have benefitted the species, facilitating invasion of the cropped area from the margins and also the spread between fields.

Neither *B. commutatus* or *B. mollis* have increased in abundance in a manner similar to *B. sterilis*, despite the similarity in many of their autecological characteristics, as summarised earlier. The reasons for this may be due to the relatively greater reduction in seed production per plant experienced by these species when in competition with a crop, especially at low weed densities. This coupled with the increased rate of seed loss, which was shown by both these species when grown in a cereal crop, may have prevented these two species benefitting from the advantages of increased dispersal in the way that

B. sterilis has, now that the restrictive practice of deep ploughing is less common. The two species would not only produce fewer seeds than *B. sterilis* but a smaller fraction of those produced will be dispersed during harvesting.

5.4 A management strategy for introductions of *B. interruptus* into cereal field headlands.

The findings reported in this thesis, as summarised earlier (section 5.2), have indicated that the headlands of fields sown with winter cereals would provide a suitable habitat for the conservation of introduced populations of *B. interruptus*. However, careful, planned management, specifically aimed at maintaining populations of *B. interruptus*, would be essential. Such a management strategy would have to consider the following issues;

1) Choice of soil type - due to the ability of *B. interruptus* to germinate at low water availabilities introductions of *B. interruptus* seed may be favoured, relative to the other three brome species considered here, on freely draining soil. Early germination would have the benefit of bestowing a competitive advantage on *B. interruptus* compared to other, slower germinating, species.

2) Initial preparation of the headland - deep ploughing, after harvesting, could be used to eliminate any brome grasses already established in the area. Dicotyledonous weeds not controlled by deep ploughing could be destroyed by selective herbicides. *B. interruptus* would be expected to germinate soon after sowing and would benefit from establishing in an area where it would initially be free from interspecific competition.

3) Control of other weeds - further studies would be necessary to indicate the importance of competition from other weed species, that would grow in a headland area, on the population ecology of *B. interruptus* . Broadleaved weeds could easily be controlled by the use of selective herbicides sprayed throughout the year. If control of broadleaved weeds proved necessary, for the maintainance of populatons of *B. interruptus*, the overall conservation value of the headland may decline due to reduced species diversity. This may

necessitate the designation of specific areas where conservation of *B. interruptus* is given priority over developing a high community diversity.

Invasion of the headland by other grasses, especially perennials, would be more problemmatic. Comparison of the life cycles of the invading grass with that of *B. interruptus* would, hopefully, indicate a possible control strategy. For example, if the invading grass was the perennial *Elymus repens* (L.) Gould control by the use of a foliar herbicide, e.g. Glyphosate, could be achieved, the herbicide being applied once the *B. interruptus* and crop were mature (and therefore, effectively dead) but whilst the leaves of *E. repens* were still green.

4) Due to the substantial fraction of the annual seed production, 45 %, of *B. interruptus* that would enter a combine at harvest and the dispersal of this seed over large distances the pattern of combining in a conservation headland would be crucial. It would be necessary to ensure that the weed seed was returned to the soil surface within the headland therefore combine harvesting would have to be parallel to the field margin for the whole of the width of the headland. Movement of weed seed into the main cropped area would be detrimental by reducing the population numbers within the headland and creating potential weed problems within the bulk of the crop, which may be intolerable to the farmer.

5) Shape of Conservation headlands - although the optimal shape and size of nature reserves has been much debated (section 1.3) in most real cases choice is severely restricted by the limits of what is available. Considering the case of conservation headlands, size will be dictated by how much productive land the farmer is prepared to manage specifically for conservation rather than monetary profits. The Game Conservancy Trust recommends the selective exclusion of pesticides from the outermost six metres of the cereal crop boardering the field margin (Sotherton, 1990). This results in the formation of long, narrow conservation areas. The theories of conservation biology indicate that circular reserves are preferable as the lower area/perimeter ratio reduces the risks of extinctions due to emigration. However, bearing in mind the limited natural dispersal of *B. interruptus* and the fact that the field margin and main cropped area are not completely hostile

environments this width of headland should be sufficient. Also careful combine harvesting along the headland would ensure that a substantial fraction of the seed produced would be dispersed within the headland itself.

6) Size of introductions - due to the large dimensions of most arable fields even 6 m wide strips running the whole length of the field will represent a large area in comparison to the area required to support individual plants (approximately 0.01 m^2 required to produce a *B. interruptus* plant of maximum size when grown in wheat, section 3.2). The field experiment (section 3.2) showed that, in the conditions of that experiment, *B. interruptus* plants grown at sowing densities between 0.5 - 10,000 seeds m^{-2} in wheat all produced seed. This indicates that the sowing density of *B. interruptus* could be choosen depending on the proportion of *B. interruptus* desired within the headland community. Further investigation, as recommended (section 5.6), would realistically be required to monitor the fate of introductions of *B. interruptus* within headlands prior to making firm recommendations as to optimal sowing rates.

5.5 Criticisms of the research

A major criticism of research of this type, that is based largely on field data, is that the results apply to only one specific set of environmental conditions, those in which each experiment was conducted. In a project of this duration, and working with an annual species, only three growing seasons can be utilised, which in effect precludes replication of any but the simplest field experiments in the interests of diversifying the range of experiments conducted. Not only were results specific to the weather conditions experienced but also to the soil type of the experimental area. As can be seen from the species distribution maps (Figure 1.4.1) *B. mollis* and *B. sterilis* are widely distributed in the U.K. which implies a broad tolerance of soil type. The distributions of *B. commutatus* and particularly *B. interruptus* are, however, more restricted. Early records of the appearance of *B. interruptus* indicated that this species frequently occurred on chalky soils (Druce, 1897). An investigation of the importance of soil type on the population ecology of these species was, however, beyond the scope of this thesis.

Only selected aspects of agricultural practices were investigated. The potential range of husbandry practices that could be studied, which would influence the population ecology of any arable weed, is enormous. Examples of such practices include the rotation of crops as opposed to continuous cereal cropping which would have major affects on species without persistent seed banks and the use of herbicides. Herbicide usage targetted at controlling dicotyledonous weeds may prove beneficial to the grass species via reduction of interspecific competition whereas herbicides designed to control grasses would be likely to prove detrimental.

5.6 Further research

One stage of the life cycle not investigated during the course of the research presented here was the fate of seed between dispersal from the parent plant and germination. The first two areas suggested for further research deal with the potential loss of seeds from the population at this stage.

B. sterilis is reported in the literature not to have a persistent seed bank (Roberts & Chancellor, 1986) however, the persistence of seed of the other three species remains untested. The survival of viable seeds for more than one year, even if only a small fraction of the annual seed production, has important consequences in terms of species persistence. Species without persistent seed banks are more vulnerable to catastrophes and this is particularly important for rare isolated populations where reintroduction by immigration is impossible. The existence of a seed bank, at a population site, also increases the effective breeding size of the population which again is important for small isolated populations (Baskin & Baskin, 1978).

Investigations on the persistence of viable seed within the soil have been conducted where seeds were buried in upturned soil filled pots (Toole & Brown, 1946) or bottles (Kivilaan & Bandurski, 1981). Retrieval, at intervals, allowed estimation of the number of seeds still viable. Similar procedures could easily be followed for all four brome species and, due to an expected lack of persistence, it would probably only be necessary to continue the experiment for a couple of years.

Seed predation, from the soil, may be a source of loss from the population. Loss of a substantial fraction (20 % from stubble surface and 13 % from shallow depth) of sown seeds was recorded in a field experiment (section 2.5). Potential predators include rodents, birds and earthworms. Worms have been shown to ingest seeds of various plant species, with noticeable differences amongst species in the numbers taken (McRill & Sagar, 1973). Some seed ingested by earthworms were found to be expelled, in a viable condition, in the wormcasts and again there were differences in number amongst species. Experiments could be either observational, recording the fate of seeds in the field, which would be time consuming and require a lot of patience, or rely on captive animals and their responses when seed was made available to them.

Although the competitive interaction of *B. interruptus* and *B. sterilis* was studied no investigation of competition amongst *B. interruptus* and dicotyledonous species typical of headlands, e.g. *Anagallis arvensis* L., *Viola arvensis* Murr., was conducted. The presence of a diversity of weed species within a conservation headland would greatly increase its overall conservation value so, if considering reintroducing *B. interruptus*, it would be important to know if this species could co-exist with a range of other weeds.

On a more academic level, the dispersal aspects of this study could be developed with the incorporation of parameters that describe the dispersal of seed into the population dynamics models that describe weeds (Firbank & Watkinson, 1985; Cousens, 1986; Cousens *et al.*, 1987) as has been recommended and reviewed by van Groenendael (1988). The addition of dispersal characteristics into a population dynamics model describing *Datura ferox* in soybean crops has been achieved (Ballaré *et al.*, 1986) which included the effects of dispersal of a fraction of seed resulting from passage through a combine harvester. A similar approach, where the seed numbers produced and the chance of emigration of seed from a defined, restricted area, could be used with the data on population dynamics (section 3.2) and the spatial dispersal from both tillage practices (section 4.3) and combine harvesting (section 4.4).

An important conclusion reported by Ballaré *et al.* (1986) was that the period of exponential population growth was extended, due to the delay in population density reaching such a level that density dependent regulation occurred, by the exportation of a fraction of the seed produced in a given area from that area. This method of modelling, including spatial dynamics, has obvious benefits, compared to using just population dynamic models, when addressing the problem of the spread of weed infestations and the possible consequences of introductions of rarities.

The final area of research that would ideally be attempted is the actual introduction of populations of *B. interruptus* into headland areas and the monitoring of these populations, along with detailed recording of the management practices used. With the permission of the Nature Conservancy Council this is an obvious next step. Introductions into real field headlands would be more informative than introductions into only partial simulations of the conditions likely to be encountered. The use of different cereal crops, spring and autumn sowing, and various cultivation practices, e.g. minimum tillage, herbicide use, could all be investigated. Regular monitoring of the introduced populations would give the best indication as to at which stage of the life cycle *B. interruptus* failed and the reasons for this failure, if it should occur.

Appendix

Appendix 1

Seed Sources

The seed stocks used throughout this project originated from the following sources;

B. commutatus	B & S Weed Seed Suppliers, Little Orchard, Wharton in the Vale, Nottingham. 1985
B. interruptus	Dr P.M. Smith, Edinburgh University, Edinburgh.
B. mollis	B & S Weed Seed Suppliers, Little Orchard, Wharton in the Vale, Nottingham. 1985
B. sterilis	Liverpool University Botanic Gardens, Ness, Wirral, Cheshire.

All seed supplies were bulked annually at the Liverpool University Botanic Gardens, Ness, Wirral, either in field conditions or in unheated polythene tunnel houses. Seed thus produced was dried naturally and stored in paper sacks, at room temperature, in darkness from the time of harvest until use. The storage room remained unheated throughout the year.

Unless otherwise stated all field experiments were conducted at the Liverpool University Botanic Gardens, Ness. The soil was of a sandy loam type that had been under cultivation for several years.

Appendix 2. Seed viability test for the four brome species conducted in October 1987.

For each species two replicates of 50 seeds were placed on moist filter paper in a Petri dish, in the dark. The number germinated, judged as the production of a radicle and coleoptile, was recorded daily until no further germination occurred. The percentage germination recorded for each species was as follows;

Species	% Germination
B. commutatus	89
B. interruptus	92
B. mollis	96
B. sterilis	90

Appendix 3. Assessment of the effects of the herbicide, Tolkan, on the four brome grasses.

Materials and Methods

Twenty plants (per pot) of each species were sprayed with the herbicide, Tolkan, a.i. Isoproturon, at a rate of 3.75 l ha^{-1} on 23.4.88. An equal number of plants were left unsprayed, as a control. Three replicate blocks were used, the pots being randomised within each block after the application of herbicide. The plants had 4-5 leaves at the time of treatment. All pots were maintained in an unheated polythene tunnel house until they were harvested on 16.5.88. At harvest the number of leaves per plant were recorded and the total above ground biomass per pot removed and dried. Biomass dry weights/pot were recorded when constant dry weight was reached.

Analysis

The mean number of leaves per plant and the dry weight biomass per pot were analysed by analysis of variance (SAS, 1985).

Results

There were no significant reductions in the mean number of leaves per plant between the herbicide treated and untreated plants (P>0.4527), Appendix Table 3.a, which indicated that there was no plant mortality. There were, however, significant reductions in the biomass per pot for three of the four species, *B. mollis* being the exception, Appendix Table 3.b. This indicated that inhibition of growth had occurred for the plants at this growth stage.

Appendix Table 3.a

Analysis of variance of mean leaf number/plant for the four brome species sprayed with Tolkan at a rate of 3.75 l ha^{-1}.

Source	d.f.	M.S.	F Ratio	$P_{(Ho)}$
Block	2	1.0152	0.68	0.5207
Herbicide	1	0.8855	0.60	0.4527
Species	3	4.0633	3.65	0.0392
Herbicide x Species	3	1.2988	0.88	0.4774
Error	14	1.4841		
Total	23	1.9062		

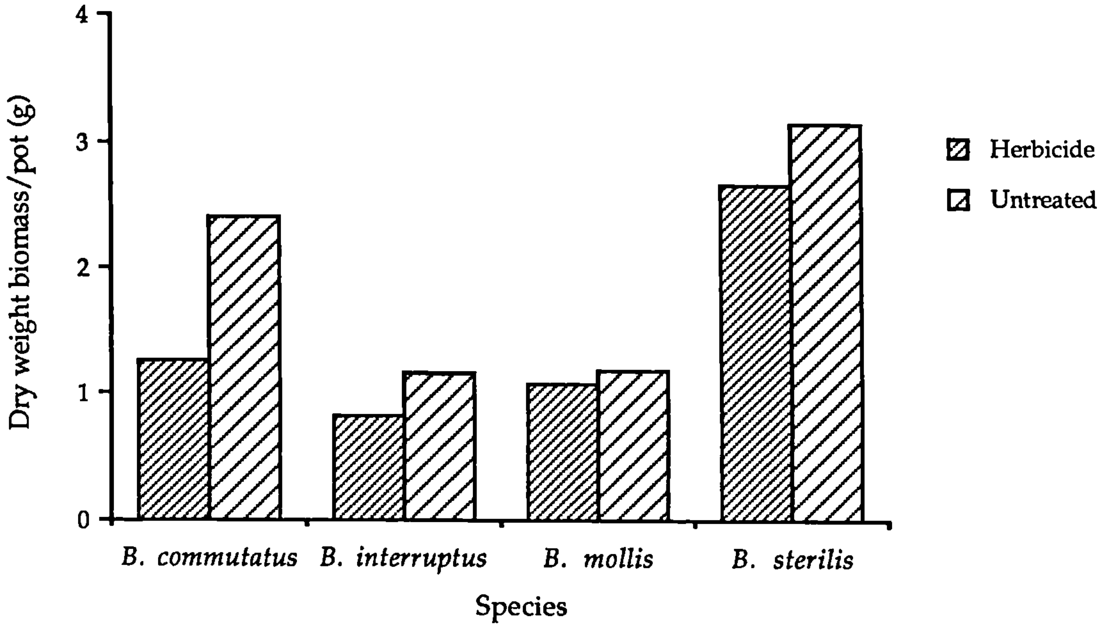
Appendix Table 3.b

Analysis of variance of dry weight biomass/pot for the four brome species sprayed with Tolkan at a rate of 3.75 l ha^{-1}.

Source	d.f.	M.S.	F Ratio	$P_{(Ho)}$
Block	2	0.4235	6.96	0.0080
Herbicide	1	1.5708	25.83	0.0002
Species	3	4.5365	74.59	0.0001
Herbicide x Species	3	0.2851	4.69	0.0181
Error	14	0.0608		
Total	23	0.7710		

Appendix Figure 3.1 The effect of the herbicide Tolkan, applied at 3.75 l ha^{-1}, on the mean biomass/pot (for 20 plants/pot) when sprayed at the 4-5 leaf growth stage.

LSD $_{(P<0.05)}$ = 0.15



Appendix 4

Table 1 Parameter estimates for the individual replicates (R) and pooled data (P) for the movement of *Brassica napus* and *Vicia faba* under three implements. The parameters quoted are M, the natural logarithm of the mean, S, the natural logarithm of the standard deviation and where appropriate, a, the origin. SE denotes the standard error of the parameter estimates.

I - Identity of fitted parameters H - Homogeneity of samples * - Significantly different at $P < 0.05$

IMPLEMENT - SPRING TINE

Species	R	a	a SE	M	M SE	S	S SE	Analysis of Chi - squared			
B. napus	1			-0.61037	0.05196	0.49877	0.04002		X^2	d.f.	
	2			-1.29756	0.06420	0.59635	0.04727	I	143.14	6	*
	3			-1.01458	0.05322	0.48185	0.04202	H	23.52	20	
	4			-0.41583	0.04531	0.43731	0.03476				
	P			-0.83636	0.03184	0.60798	0.02447				
V. faba	1			-0.57214	0.05306	0.51086	0.04174				
	2			-0.82583	0.08098	0.78624	0.06267	I	43.14	6	*
	3			-0.94251	0.08640	0.83204	0.06658	H	63.59	28	
	4			-1.09766	0.07996	0.76258	0.06228				
	P			-0.85820	0.03892	0.75195	0.02992				

IMPLEMENT - SEED DRILL

B. napus	1	-0.34355	0.13641	-0.97658	0.39647	0.40027	0.14808				
	2	-0.20598	0.06083	-1.63776	0.39884	0.59296	0.20016	I	93.11	9	*
	3	-0.40651	0.20167	-0.78537	0.46339	0.25657	0.12106	H	2.78	8	
	4	-0.13468	0.01550	-2.06108	0.27393	0.80046	0.18994				
	P	-0.24560	0.04178	-1.32923	0.18740	0.49825	0.08646				
V. faba	1			-2.08319	0.10021	0.82697	0.09330				
	2			-2.05284	0.06496	0.54127	0.06483	I	22.42	6	*
	3			-2.13188	0.07541	0.60869	0.07263	H	11.62	12	
	4			-2.51297	0.15978	1.05361	0.14789				
	P			-2.16082	0.04672	0.74937	0.04464				

Appendix 4 Table 1 continued

IMPLEMENT - ROTIVATOR

Species	R	a	a SE	M	M SE	S	S SE		X^2	d.f.	
		Parameter Estimates						**Analyis of Chi-squared**			
B. napus	1	-0.17163	0.07283	-0.35914	0.16385	0.83305	0.12354				
	2	-0.35599	0.10353	-0.72224	0.24469	0.50966	0.11598	I	100.60	9	*
	3	-0.47370	0.13339	-0.10353	0.18857	0.67944	0.11473	H	42.42	72	
	4	-0.20790	0.03945	-1.13850	0.17701	0.70939	0.11646				
	P	-0.24283	0.02652	-0.70192	0.08481	0.84537	0.06207				
V. faba	1	-0.15801	0.02282	-1.31754	0.19283	1.05628	0.16403				
	2	-0.13443	0.06212	-1.02989	0.21267	0.75718	0.12824	I	48.95	9	*
	3	-0.16989	0.02920	-1.58944	0.24943	0.92841	0.18219	H	30.12	24	
	4	-0.16024	0.02592	-1.48006	0.17465	0.67134	0.11766				
	P	-0.17033	0.01379	-1.29881	0.09032	0.86195	0.06918				

Appendix 4

Table 2 The parameter estimates for individual replicates (R) and pooled data (P) for four species under the passage of two implements.. The parameters quoted are M, the natural logarithm of the mean, S, the natural logarithm of the standard deviation and, where appropriate, a, the origin. SE represents the standard error of the parameter estimate.

I - Identity of fitted parameters H - Homogeneity of samples * - Significantly different at $P < 0.05$

IMPLEMENT - SPRING TINE

				Parameter Estimates		Analysis of Chi-squared					
Species	R	a(m)	a SE	M	M SE	S	SE		X^2	d.f.	
B. sterilis	1			-1.15701	0.08513	0.80332	0.06556				
	2			-1.01519	0.07302	0.68645	0.05503	I	27.12	6	*
	3			-0.93711	0.05445	0.49608	0.04273				
	4			-0.93057	0.08726	0.83119	0.06829	H	41.48	28	
	P			-1.01115	0.03796	0.71690	0.02892				
B. interruptus	1			-1.20667	0.05728	0.48999	0.04087				
	2			-1.47693	0.09625	0.88839	0.07782	I	30.26	4	*
	3			-1.41589	0.08469	0.78228	0.06667				
	P			-1.36334	0.04508	0.72151	0.03418	H	24.74	21	
A. githago	1			-1.34006	0.07539	0.69422	0.05772				
	2			-1.96564	0.12001	0.99582	0.10976	I	39.14	6	*
	3			-1.24994	0.10215	0.96168	0.08438				
	4			-1.61343	0.09595	0.86804	0.08131	H	50.46	28	
	P			-1.53098	0.04956	0.90635	0.04169				
B. napus	1			-1.31743	0.07977	0.74110	0.06220				
	2			-1.88320	0.06990	0.59678	0.06331	I	72.10	4	*
	3			-1.05130	0.05995	0.54338	0.04556				
	P			-1.41943	0.04547	0.72389	0.03569	I	21.94	21	

Table 2 continued

Parameter Estimates Analysis of Chi-squared.

IMPLEMENT _ ROTIVATOR

Species	R	a	a SE	M	M SE	S	S SE		X^2	d.f.	
B. sterilis	1	-0.24078	0.05106	-0.91146	0.18377	0.73401	0.12501				
	2	-0.24781	0.06062	-1.21756	0.27248	0.73018	0.16610	I	42.43	12	*
	3	-0.13348	0.02603	-1.64712	0.18833	0.83007	0.13710				
	4	-0.22097	0.04757	-1.34470	0.26982	0.88163	0.18336	I	23.48	40	
	5	-0.23017	0.05100	-1.07243	0.23444	0.91257	0.17215				
	P	-0.21043	0.01863	-1.24838	0.10158	0.84960	0.07201				
B. interruptus	1	-0.16405	0.05163	-1.26224	0.21330	0.61609	0.12097				
	2	-1.09458	1.00081	0.18657	0.84879	0.27518	0.20991	I	38.79	6	*
	3	-0.56168	0.27871	-0.31902	0.41037	0.38452	0.14776				
	P	-0.51422	0.12010	-0.43553	0.20037	0.40268	0.07527	H	12.73	24	
A. githago	1	-0.33444	0.10501	-0.83312	0.29475	0.66459	0.16607				
	2	-0.45346	0.16124	-0.55570	0.30739	0.42470	0.12187	I	39.98	12	*
	3	-0.22847	0.05526	-1.57830	0.35866	0.91937	0.22432				
	4	-0.24772	0.06720	-1.38305	0.33178	0.60253	0.16990	H	12.48	40	
	5	-0.22143	0.05213	-1.63240	0.36336	0.96673	0.23237				
	P	-0.27314	0.03260	-1.19226	0.13556	0.72588	0.07847				
B. napus	1	-0.25513	0.07889	-1.50926	0.42857	0.69262	0.22042	I	7.07	3	
	2	-0.47838	0.26131	-0.69412	0.54924	0.29364	0.15298				
	P	-0.30835	0.07702	-1.20467	0.29198	0.51240	0.12644	H	1.97	16	

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