SESSION 4A

WEED BIOLOGY AND THE CHARACTERISTICS OF INTRACTABLE WEEDS

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INVITED PAPERS	4A-1 to 4A-7

INTRACTABLE WEEDS--INTRASPECIFIC VARIATION MUST BE CONSIDERED IN FORMULATING CONTROL MEASURES

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ABSTRACT

Intractable weed species are often characterized by great intraspecific variability. The importance of such variability in formulating control measures is discussed with particular reference to a) resistance to herbicides, b) susceptibility to parasites and pathogens, c) seed dormancy and longevity, d) phenology and life span, and e) the structure and function of clonal growth organs. One species, *Panicum miliaceum* (proso millet) is examined in detail.

A brief examination of almost any temperate-zone flora will show clearly that many weed species must be included amongst the most variable in the entire list. Most of the common ones are represented by several varieties or subspecies and even the ones that seem to have only a single, clearly defined biotype often assume radically different phenotypes in different habitats. As an example, Brenda Frick working in my laboratory at the University of Western Ontario made a survey of the larger angiosperm families within our local flora (Gleason 1963). She was looking for species with multiple life cycle strategies (i.e. more than one of annual, biennial and perennial). She found that out of 2529 species, only 88 or approximately 3% had more than a single life cycle strategy. Although few in absolute number, they represented 11 of the 30 families examined. Most of these 88 were common weeds.

Weedy species are variable in many ecologically and agronomically important respects including phenology (Law *et al*. 1977, Putwain *et al*. 1982), ability to spread clonally (Leakey 1981), susceptibility to parasites and pathogens (Hasan 1981), amount of seed dormancy (Cavers and Harper 1966) and resistance to herbicide application (Bandeen *et al*. 1982, Gressel *et al*. 1982). This intraspecific variability must be kept in mind when control measures are being formulated since a measure that will work with one population of a species, may have little or no effect on a second population of the same species.

In this paper, I will be discussing a number of ways in which intraspecific variation in weed species has rendered these species intractable to straightforward control measures. I will conclude by examining one exceedingly variable species, proso millet (*Panicum miliaceum* L.). This grass, a major crop in Asia and Europe, has become a serious and intractable weed in North America within the past 20 years.

Herbicide Resistance in Weedy Species

Within five years of the introduction of 2,4-D and related compounds there were scattered reports of intraspecific differences in susceptibility in certain weed species (Stryckers 1958 (cited in Gressel *et al*. 1982), Sexsmith 1964, LeBaron 1982). In some of these species the susceptible and resistant biotypes differed in visible morphological features but in others the two kinds of biotype were indistinguishable except in terms of their response to herbicides. It has become evident that in species such as

Cirsium arvense some plants escape herbicide damage because their excessive hairiness prevents herbicide contact with sensitive tissues (P. Marriage, personal communication) whereas in other species the difference in herbicide response is found at the cellular or sub-cellular level.

There have been many recent reports of intraspecific differences in herbicide tolerance, particularly with reference to triazine herbicides (Bandeen *et al*. 1982, Gressel *et al*. 1982). At present herbicide tolerant populations do not cause the reductions in crop yields that might be expected because they are usually reduced easily by an alternative herbicide (Bandeen *et al*. 1982). Bandeen *et al*. (1982) further suggest that crop rotation and the use of at least one cultivation per year "may be preventing or delaying the exponential increase in seed populations of triazine-resistant weeds" that might be expected in areas such as the United States corn belt.

It may only be a matter of time before more serious problems of herbicide-resistance appear. For example, continual alternation between two classes of herbicide may eventually give us a single weed population that is tolerant of both types. Gressel *et al*. (1982) report that *Poa annua* is already represented by populations resistant or tolerant to triazine herbicides in France; to paraquat, a bipyridylium herbicide, in England, and to metoxuron, a urea, in experiments in Europe. *P. annua* in England also has triazine-resistant populations (P. Putwain, pers. comm.).

Susceptibility to Pathogens

During the past ten to fifteen years some attempts to control weeds by biological methods have only been partially successful. Some weed populations have been decimated but other biotypes of the target species have not been damaged. A noteworthy example is the skeleton weed project in Australia.

In 1971 Australian scientists introduced a rust fungus *Puccinia chondrillina* for the control of skeleton weed, *Chondrilla juncea*. The strain of *P. chondrillina* that was used brought about great reductions in the narrow-leaved form of *C. juncea* but the intermediate- and broad-leaved forms of the weed were not attacked (Hasan 1981). Unfortunately, the vacant niche created by the reduction of the narrow-leaved form was filled by plants of the other two forms of *C. juncea* (Groves 1984). Subsequent searches in the Mediterranean region have discovered strains of *P. chondrillina* which are highly virulent against the intermediate-leaved form of *C. juncea* and one strain from western Turkey has been introduced into Western Australia where the intermediate-leaved form is common (Hasan 1981).

Attempts to control skeleton weed with the same fungus in the western United States revealed greatly different responses to infection by *P. chondrillina* in populations of *C. juncea* from California, Washington, Idaho and Oregon (Emge *et al*. 1981).

Variation in host weed species has also led to problems in achieving control of such weeds as *Carduus nutans* (Zwölfer and Harris 1984); the *Euphorbia esula-virgata* complex (Harris 1981) and *Plantago lanceolata* (Alexander 1983). In some species such as *Xanthium strumarium* (Hare and Futuyma 1978) intra-populational variation in plant chemicals as well as variations in morphological features such as fruit (burr) size cause considerable variation in the resistance of individual plants to insect seed predators. Obviously, intraspecific differences in weed species will have to be considered carefully in any future attempts at biological control.

Seed Dormancy

The pattern of germination exhibited by seeds of a species is usually important to the effectiveness of that species as a weed. Seeds that germinate when control programs are difficult or ineffective will have an enhanced chance of continued survival. Greater variability or intermittency in seed germination often improved the weed population's success, since each time that a stand of seedlings or older plants is destroyed, a new stand will soon arise from the seed bank to take its place (Cavers 1974).

Within some species variability is increased by between-population differences in the patterns of germination. For example, van der Vegte (1978) identified two populations of Stellaria media growing together in newly abandoned arable fields in Holland. Virtually all seeds from one population germinated soon after production or died, whereas the seeds from the second population had a broad range in amounts of dormancy and gave rise to a prolonged intermittent pattern of seedling emergence.

Cavers and Harper (1966) and several later workers have shown that plants within a population can vary greatly in the germination response of their seeds. Salisbury (1963) found that seeds from a single plant of Capsella simplex produced a strongly intermittent pattern of germination, with some seedlings emerging in each of eight successive months after sowing in an unheated greenhouse in England.

The late Dr. J. M. Naylor spent many years unravelling the very complex nature of dormancy within wild oats (Avena fatua) on the Canadian prairies. This species exhibits great variability in seed dormancy and in the length of viability of dormant seeds in the soil (Naylor 1983). There is much genetic variability in this species and the duration of seed dormancy is controlled by several to many genes (Naylor 1983). Sawhney and Naylor (1982) have also shown that the genetic variability is supplemented by great phenotypic plasticity in seed dormancy. Thus the same genotype growing under different climatic conditions in different sites, or in the same site in different years, could produce seeds with great differences in dormancy. These findings by Naylor and his co-workers explain why the germination patterns of Avena fatua show wide variation from place to place across the prairies.

Phenology and Life Span

Many weed species are widely distributed around the world and because they occur over vast distances cosmopolitan species such as Stellaria media, Poa annua and Taraxacum officinale are known to show great variation over their range in many morphological and physiological attributes (King 1966). Some of the most important differences between distant populations may be in phenology; differences in the date of resumption of growth in the spring, in the date and duration of flowering, in the length of the seed-ripening period, etc. Such variation within a widely distributed species could mean that a method of control which works well in one country might have little effect on the same species in a second country or perhaps on a different continent. For example, Sorghum halepense, listed as one of the world's ten worst weeds, has great variation with its range. It has been described as having latitudinal ecotypes, physiological ecotypes, morphological ecotypes and geographical variants within its native range (Warwick et al. 1984).

Hume and Cavers (1982ab, 1983ab) examined populations of Rumex crispus from a wide latitudinal and climatic gradient within North America. They found that most of the variation between plants could be attributed to phenotypic plasticity and within-population variation (Hume and Cavers 1982a).

Nevertheless, plants in contrasting areas differed in characters which could greatly influence the response to control measures (Hume and Cavers 1982b). For example, plants on coarse-textured soil were small and spreading and would not be as suitable for "roller-wick" herbicide treatments as the taller, more upright plants on silt and clay soils. Plants from dry regions had highly overlapping, appressed branches and relatively small stomata; attributes that could influence the amount of herbicide uptake. Plants from dry, warm areas (e.g. Texas) also produced much larger achenes (seeds) (Hume and Cavers 1983a) and these would have different dormancy and seedling characters. The populations also differed greatly in response to photoperiod, requirements for vernalization and in life span (Hume and Cavers 1983ab). Thus some populations of the species were annuals or short-lived perennials while all plants in other populations required a winter experience before flowering could occur. Such differences have obvious implications for control.

Of greater importance in local situations are the co-occurrences of either two or more distinctly different populations, or highly variable single populations of one species. For example, Plantago major is represented in many temperate regions by two distinct subspecies; ssp. major is longer lived, more competitive and occurs in perennial plant communities which are regularly mown (lawns, roadsides) while ssp. pleiosperma is short lived, matures rapidly and occurs primarily in arable land (Molgaard 1976 and pers. comm.). Warwick (1979) described two main variants for Poa annua which co-occur in many habitats in North America and Europe. One variant includes quick-flowing, short-lived plants with erect growth while the second is represented by prostrate or semi-prostrate perennial plants which flower and fruit more slowly. Such intraspecific differences allow occurrence in a greater variety of agricultural habitats. Methods of control used in one habitat might be entirely impractical in a second habitat.

Many weed species in temperate regions have annual and winter annual forms. In a number of these species, there is intermittent seedling emergence throughout the growing season. Early seedlings flower and set seeds in the same season but the later-arising seedlings generally do not flower until the following spring (e.g. Lappula squarrosa (Frick 1981)). In Thlaspi arvense McIntyre and Best (1975) identified two genetically distinct populations from the same fields. Because these two populations differed in the length of the pre-reproductive period, the early flowering plants were strictly summer annuals while the late-flowering population consisted primarily of winter annuals. In growth chamber experiments Best and McIntyre (1976) found that young seedlings of the late-flowering type could be vernalized and made to behave as summer annuals.

Repeated use of the same control measures over a number of years can change the general phenology of weed populations. For example Putwain et al. (1982) showed that repeated use of simazine led to much later flowering periods each year in populations of Senecio vulgaris. Darmency and Aujas (1985) studied the proportions of early flowering (spring) and late-flowering (winter) types of Avena fatua in a field in France that was kept under continuous winter cropping. In six years the proportion of winter type plants increased from under 20% to nearly 50% of the total population. Examples such as this show how the variability within weed species enables them to survive in an area.

4A—1

The Structure and Function of clonal Growth Organs

Weedy species that can be propagated by clonal growth as well as by seeds benefit for several reasons: 1) Clonal growth enables a population to spread within a local area that is favorable for the genotypes that are present. 2) Clonal growth structures often have dormancy which delays regrowth or sprouting until a favorable period for such growth occurs. In several cases establishment from clonal structures occurs at different times from establishment from seed. 3) Clonal growth structures are often large and filled with nutrients. Thus the new individuals arising from these structures can be much more vigorous than a seedling of the same species. 4) Production of clonal growth organs can take place during a period (e.g. autumn) when flowering and seed production are not occurring on the same plant. The resources used for clonal growth would largely be non-utilized if clonal growth did not occur.

Leakey (1981) stated that "very little is known of the varying ability within species to regenerate vegetatively" but despite this statement he reported such variability for *Arrhenatherum elatius*, *Ranunculus repens*, *Elymus repens*, *Bellis perennis*, *Taraxacum officinale*, *Festuca rubra* and *Trifolium repens*. Warwick *et al*. (1984) found that a few populations of *Sorghum halepense* could overwinter as rhizomes in Southern Ontario, Canada. These populations differed greatly in morphological and physiological characters from the much more numerous populations which could overwinter only as seeds. The former populations produced ten times the amount of rhizome tissue per plant. Degennaro and Weller (1984) collected five 'presumed biotypes' from a single field population of *Convolvulus arvensis* near Lafayette, Indiana, U.S.A. These biotypes differed enormously in their potential for vegetative propagation (e.g. from 1.8 to 74.5% of the root buds per population developed into shoots of new ramets) These authors suggested that the great variability in growth and reproduction shown by the different biotypes could explain the ability of this species to survive and adapt to changes in environmental conditions and control practices.

Some weed species can produce more than one kind of clonal propagule. Leakey (1981) suggests that the success of such species can often be attributed to the combination of methods of vegetative regeneration that they possess. For example, *Allium vineale* produces bulbs, offsets and bulbils (Leakey 1981). *Cynodon dactylon* has both underground (rhizomes) and aboveground (stolons) means of clonal growth. The rhizomes and stolons differ greatly in tolerance of tillage (Håkansson 1982). The proportion of rhizomes and stolons differs considerably within the species and Håkansson (1982) attributes this variation to both environmental and biotype differences. In *Barbarea vulgaris* vegetative regeneration can occur through development of new ramets from root buds, regrowth of the crown, or through the production of cauline rosettes on the flowering stalk after seed formation (MacDonald and Cavers 1974). The incidence of these various structures varies from one habitat to another but there did not seem to be differences in occurrence of cauline rosettes between plants of two varieties of *B. vulgaris* when they were grown in a common garden (MacDonald and Cavers 1974).

Recently, we have been examining variation within Jerusalem artichoke (*Helianthus tuberosus*). This species occurs as a weed in Southern Ontario. It spreads locally through the production of both rhizomes and tubers and there is great variation in both rhizome and tuber structure among weed populations. Variation between biotypes occurs in the size and vigor of tubers; the amount of sprouting of rhizomes in the summer of production, the rates of decay of both tubers and rhizomes and in the duration of after-ripening needed before sprouting can occur from rhizomes (C.J. Swanton, unpublished).

Proso millet (Panicum miliaceum), a intractable and variable weed

I will use proso millet as a prime example to illustrate the variability that can be found within a single weed species and to show why this variability must be considered in formulating methods for controlling the species. Proso millet has a long history as both a crop and a weed in Europe and Asia (Rachie 1975; Lysov 1975). It came to North America with the earliest European settlers and is still grown as feed for livestock and wild birds (Strand and Behrens 1979). In Canada it is a serious weed in corn fields, especially in Manitoba and Ontario.

It is noteworthy that different biotypes are important as weeds in different parts of Canada (Table 1). The two most serious and extensive infestations are caused by the crown biotype in Southern Manitoba and the black biotype in Southern Ontario. For a detailed description of the major weed biotypes see Bough et al. (1986). Many of these biotypes are derived from crop varieties originating in different parts of the world but the black-seeded biotype seems to have been an agriculture weed for hundreds, if not thousands, of years (Cavers and Bough 1985).

Attempts to control weed populations of proso millet would have better chances of success if the biotype or biotypes present could be identified first (see Table 1). For example, biotypes that are attractive to wild birds could be greatly reduced in numbers as long as the (freshly produced) seeds are available above the soil surface. Also fields with non-shattering crop-like weeds such as the white, golden, or orange-red biotypes could be harvested with small-grain equipment (which is cleaned carefully afterwards) and the seeds could be fed to livestock. However, attempts to do this with the freely-shattering black-seeded biotype would only serve to disperse the seeds over a wider area. Fields contaminated with biotypes such as white or orange-red could be planted to pasture or small-grains for two to four years and this would lead to virtual elimination of the proso millet seed bank. A similar procedure in fields contaminated with the highly dormant black or dark red biotypes would still leave sizeable seed bank populations capable of producing new infestations.

In contrast, the application of a herbicide such as "Fusilade" (fluazifop-butyl) should give a significant reduction in a population of the black-seeded weed but would probably have much less effect on a population of the white-seeded crop-like weed.

In summary, the great variation that is found with Panicum miliaceum can be traced to conscious selection in agriculture for certain attributes (large seed size, non-shattering, non-dormant seeds, etc.) in the crop varieties and unwitting selection of weed biotypes with strong seed dormancy, smaller seeds, freely-shattering inflorescences, etc. The two biotypes that cause widespread weed problems in Canada ('crown' in Manitoba and the black-seeded weed in Ontario) differ from each other in most of the characters discussed above. The methods appropriate for control of the one biotype are quite different from those appropriate for the other.

CONCLUSION

I predict that the problem of intraspecific variability in weed species will become more important in the near future. My first reason for this conclusion is that the rate of introduction of plant species (and biotypes

Table 1. The weed populations of proso millet in Canada, with a summary of characters important for identification and survival. (--- denotes not tested)

	Seed Characters					Plant Characters					
BIOTYPE	Where Found in Canada	Seed Colour	Mean Weight per Seed (mg)	Seed Dormancy	Palatability to Birds	Seedling Vigour	Time to Maturity	Tillering	Herbicide Tolerance	Panicle Shape	Shattering
Black	Southern Ontario	Dark olive green to dark brown to black	3.0 to 4.2, in mid-season 3.9 ± 0.2	Strong in fresh seeds, viable for more than 5 yr. in soil	Extremely distasteful, regurgitated if eaten by mistake	Least	mid-range, 7-8 weeks for first mature seeds	moderate, stronger in open-grown plants	Most successfully controlled, little difference between populations	Open, obvious pulvini	Seeds shatter readily as they mature
Crown	Southern Manitoba plus scattered populations in Ontario and Quebec	Grey-green with lighter yellowish cream stripes	Varies greatly, from 4.3 to 6.6 in different populations	Little inherent dormancy, a few seeds survived 2 yr. in soil	Low, only black seed less palatable	moderate to strong	42-50 days, Manitoba populations fastest of all	moderate, open-grown plants tiller readily	More resistant than black, variable between populations	Open, pulvini present	most populations do not shatter readily
Golden	Southern Ontario and Southern Quebec	Golden yellow, variable between populations	Varies from 4.9 ± 0.25 to 5.9 ± 0.23 in different populations	Little or none, some seeds germinate in autumn after production	palatable	moderate to strong	one week later than black in producing mature seeds	little tillering, but one population tillers strongly	More resistant than black, variable between populations	Contracted panicle, bent to one side	Does not shatter
Dark Red	Southern Quebec, vicinity of Montreal	Dark reddish brown	5.2 ± 0.2	Strong in fresh seeds and in soil after 7 mo. overwinter	---	---	---	Moderate unless lodged when vertical shoots appear at nodes	---	Contracted but more open than white, golden or orange-red	Little shattering
Orange-Red	Scattered populations in Manitoba, Ontario and Quebec	Bright orange-red	6.2 ± 0.25	Little dormancy	most palatable as crop	---	mid-range, similar to golden	Tillers profusely always, shortest biotype	More resistant than black, to 'Fusilade' but very susceptible to 'Dowco 453'*	Intermediate in panicle openness	Little shattering
White	Only persistent weed population is in Eastern Ontario	Light cream to ivory	6.0 ± 0.25	Least of all populations tested	very palatable as crop	--- (white seeded crop has strong vigour)	---	sparse	Most resistant	Contracted, droops to one side	Does not shatter
Elgin	One small population only. Elgin Co. South-western Ontario	Light golden	6.5 ± 0.5	Weak, but some seeds survive one year in soil	palatable, favoured by goldfinches	---	last to mature, largest and tallest plants	sparse	Easily controlled, but more resistant than black	Long but compact, droops to one side	Little shattering

within species) to new areas has been increasing during the past century and has risen sharply in the last twenty to thirty years (Forcella 1985).

After a new biotype becomes established in an area there is the distinct probability of hybridization with biotypes that are already present and this will lead to even more intraspecific variability. As an example I have looked at the distribution of several Rumex species in the prairie provinces of Canada. During the period of settlement Rumex species (docks) from Eastern Europe and Asia were inadvertently introduced along with several species of the same genus which are common in Eastern North America and Western Europe (e.g. Rumex crispus, R. obtusifolius). Many of these species survived and in addition there are now many kinds of fertile interspecific hybrids.

Another cause of increased intraspecific variability is the introduction of new methods of weed control. With every new method, there is usually a corresponding increase in a weed biotype that fills the newly-created niche. Where the only substantial populations of such weeds as Chenopodium album used to be triazine-susceptible, there are now large triazine-resistant populations plus large triazine-susceptibile populations remaining in areas which have not had repeated applications of triazine herbicides. Putwain et al. (1982) found greater variability in the phenology of Senecio vulgaris after some populations were subjected to repeated applications of simazine.

Finally, there are several species that are in use or being tested as crops, and because there is new or renewed interest in the species a variety of plant breeding techniques are being used to produce new varieties. At the same time the same species occur as weeds in the same or other areas. Panicum miliaceum is one example. Some of the new crop varieties might well become weeds, thus adding to the variability within the weed populations of that species.

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INTRACTABLE WEEDS: A FAILURE TO APPRECIATE ECOLOGICAL PRINCIPLES IN WEED CONTROL ?

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ABSTRACT

Intractable weed species are those which from a management standpoint do not decline to acceptable levels in the face of existing control procedures. Where control measures rely on, or are influenced by, biotic interactions within agro-ecosystems, appreciation of the population dynamics of weed species is necessary to explain the relative efficacy of control measures. It is argued that interactions between intrinsic mechanisms of population regulation and weed control practices may result in intractability. These views are illustrated by experimental studies of *Avena fatua* and *Bromus sterilis*.

INTRODUCTION

The Shorter Oxford English dictionary defines 'intractable' as 'not easily treated or dealt with .... resisting treatment or effort'. For weed species, it remains a relative term in the sense that certain species are recognised to be injurious and to coexist with a crop as an integral biotic component of a *specific* agro-ecosystem. The characteristics of an agro-ecosystem are determined by the type and pattern of cropping and the husbandry practices aimed at the control, if not elimination, of weeds, pests and diseases. Thus in the 1940's, many dicotyledenous species were perceived as intractable before the advent of chemical control measures. In modern agro-ecosystems intractable species are those which persist at damaging infestation levels in the face of chemically reliant husbandry practices which are designed to minimise heterogeneity in the physical and biotic components of the crop environment.

Intractability in a weed species may result for two principal and interrelated reasons. Genetically both the possession of genes for herbicide tolerance or resistance (Lebaron and Gressel,1982) and those enabling crop mimicry (Barrett,1983) will render weed species difficult to control. Ecologically it is the possession of a life history pattern which enables a weed species to have positive ecological fitness within an agro-ecosystem that confers intractability. This review focuses on the ecological determinants of intractability in weeds concentrating on annual homogeneous cropping systems.

THE ECOLOGICAL SETTING FOR INTRACTABILITY

Most modern cropping systems present to a weed species a habitat with frequent and highly predictable (often seasonal) perturbations (Snaydon,1980). Arable ecosystems are exemplary. Pronounced disturbance of short duration during seed bed preparation is followed by a long period in which competitive pressure from the crop is intense, gradually diminishing with crop maturation before harvest. Between removal of plant biomass at harvest and subsequent seed bed preparations, a length of time exists when resources for plant growth are often sufficient for the success of short lived ephemeral species.

Ecologically therefore, intractable species may be those that either display a life-cycle broadly synchronised with the growth of the crop (e.g. *Galium aparine* and *Avena fatua* in cereals) or those that undergo generation turnover in the late life of the crop or in the fallow period between cropping sequences (e.g. *Poa annua* and *Stellaria media*). The damage done to the crop by these two classes of weed species may well be unequal. Whilst the former contribute to almost all components of the damage function (Mortimer,1984) and particularly yield loss, species which grow and reproduce late in the cropping season and in arable stubbles may contribute a smaller amount to the overall damage accruing from weed presence (perhaps through matter other than grain at harvest (Elliott,1980) but largely by seed bed infestation). Such a comparison is largely conjectural; no one to my knowledge has critically assessed the individual species' contributions to crop damage exerted by the weed flora for all damage components.

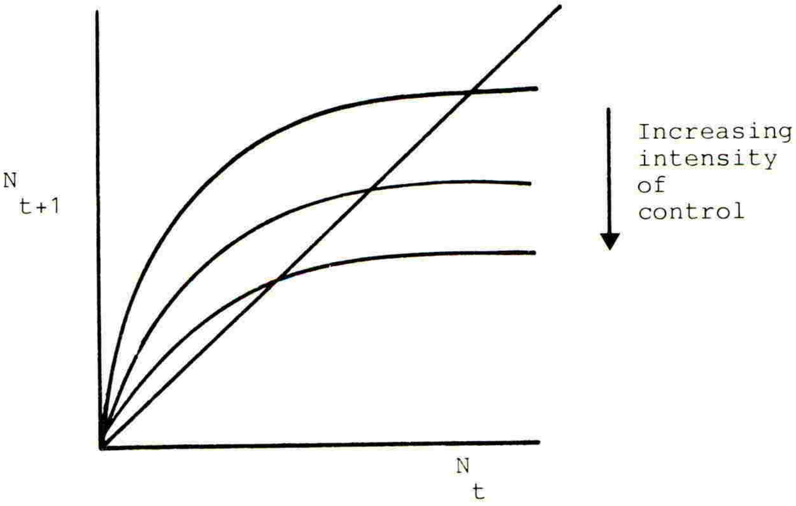
Weed species occupying the habitat when crop growth is not occuring, though not commonly considered intractable, nevertheless require routine control for cost at seed bed preparation to ensure maximum crop establishment after seeding. More conspicuous intractable species are those which co-occur with the crop for much or all of its life despite historically prolonged attempts to control them. Of these grass weeds in arable agro-ecosystems predominate (Froud-Williams and Chancellor,1982) and provide useful exemplars for study.

If a weed species exhibits positive fitness in a habitat, then populations will either grow in size or at least maintain equilibrium population sizes. Elucidating the factors

$ a finite rate of increase $\geqslant 1$.

determining population size and regulating the rate of growth of the population requires a demographic understanding of how one generation of a weed species maps onto another , Fig. 1. Of particular concern are 1) whether, for particular management regimes, intractable species are maintained at stable equilibrium and 2) the relative roles of density dependent (self regulating) and density independent factors and their interactions. It is a subject about which we still retain remarkable ignorance for many weed species. Yet some observations are possible and, with quantitative knowledge, will produce explanations of why specific weed species remain intractable.

Fig.1. Conjectural maps of changes from generation to generation in weed populations. Censuses in each population (N_t and N_{t+1}) are taken at the same point in the life cycle and population sizes are assumed to be intraspecifically regulated. Equilibrium population sizes are indicated by the intersection with the diagonal line of unit slope.



Population equilibria

The existence of stable equilibria in field populations of intractable weed species has yet to be convincingly demonstrated. Moreover there are several reasons for suspecting that stable equilibria will be rare : individuals in weed species populations are characteristically dispersed heterogeneously within a crop; control practices are rarely pursued with the same frequency and intensity over several cropping seasons; continuous monospecific cropping may not be employed; and migration of seed from field margins and hedgerows may be a significant but variable feature (Marshall, 1984). In consequence at the level of the field population weed species may rarely be seen to be at stable equilibrium. Populations may fluctuate temporally and spatially within limits prescribed by management practices. Populations may appear to fluctuate unpredictably and the species be intractable to control. Disentangling the process requires investigation of the role of all factors influencing population size and particularly those that are density dependent.

FACTORS REGULATING THE SIZE OF WEED POPULATIONS ILLUSTRATIONS WITH TWO GRASS WEEDS.

Fig. 2 illustrates generation maps for *Avena fatua* in monoculture and under two cropping regimes, winter wheat and spring barley. This species remains difficult to control in cereals for three reasons : the presence of a long-lived buried seed population (mean half-life 523 days; Manlove,1985); episodic recruitment of seedlings ; and high reproductive capacity. In a single generation, populations of 10 seeds per square metre may increase by three orders of magnitude when growing alone and approximately two orders regardless of whether the companion crop is autumn or spring sown. Moreover in both winter wheat and spring barley populations arising from high infestation densities (> 10^4 seeds m.$^{-2}$) achieved equal size in the subsequent season, despite the fact that the start of plant recruitment in spring barley was delayed by 14 weeks in comparison to populations in winter wheat. Elevated survivorship of *A. fatua* seedlings, and the positive fitness of individuals in very late emerging cohorts (May and June) were significant contributory factors. The compensatory responses to increasing density exhibited by *A.fatua* (Fig. 2) are a consequence of two density dependent regulatory periods in the life cycle - 1) the transition from seed to seedling and 2) seed production by adult plants (Manlove,1985). This density dependent regulation extended over the range of 10 - 30000 seeds m.$^{-2}$ (census point, late summer post seed dispersal). It is against this background that the effects of control measures must be examined. Clearly, reduction of the seedling population will result in enhanced compensating seed production. Conversely reducing seed production by adult plants will be met in the next generation by less intense density dependent regulation of seedling populations.

The consequences of spraying a post-emergence herbicide, l-flamprop-isopropyl, on *A. fatua* dynamics is shown in Fig.3. Rates of increase declined monotonically with increasing infestation density to equilibrium population sizes (given constancy both seasonally and in management practice) of 33,000 and 8,300 seeds m.$^{-2}$ in monoculture and winter wheat respectively. Application of the herbicide to *A. fatua* in winter wheat reduced the rate of increase by an equivalent order of magnitude as the competitive effect of the wheat

Fig.2. Generation maps for <u>Avena fatua</u> growing in monoculture, winter wheat and spring barley for the season 1981-1982. Populations are censused in late summer after seed dispersal (from Manlove,1985).

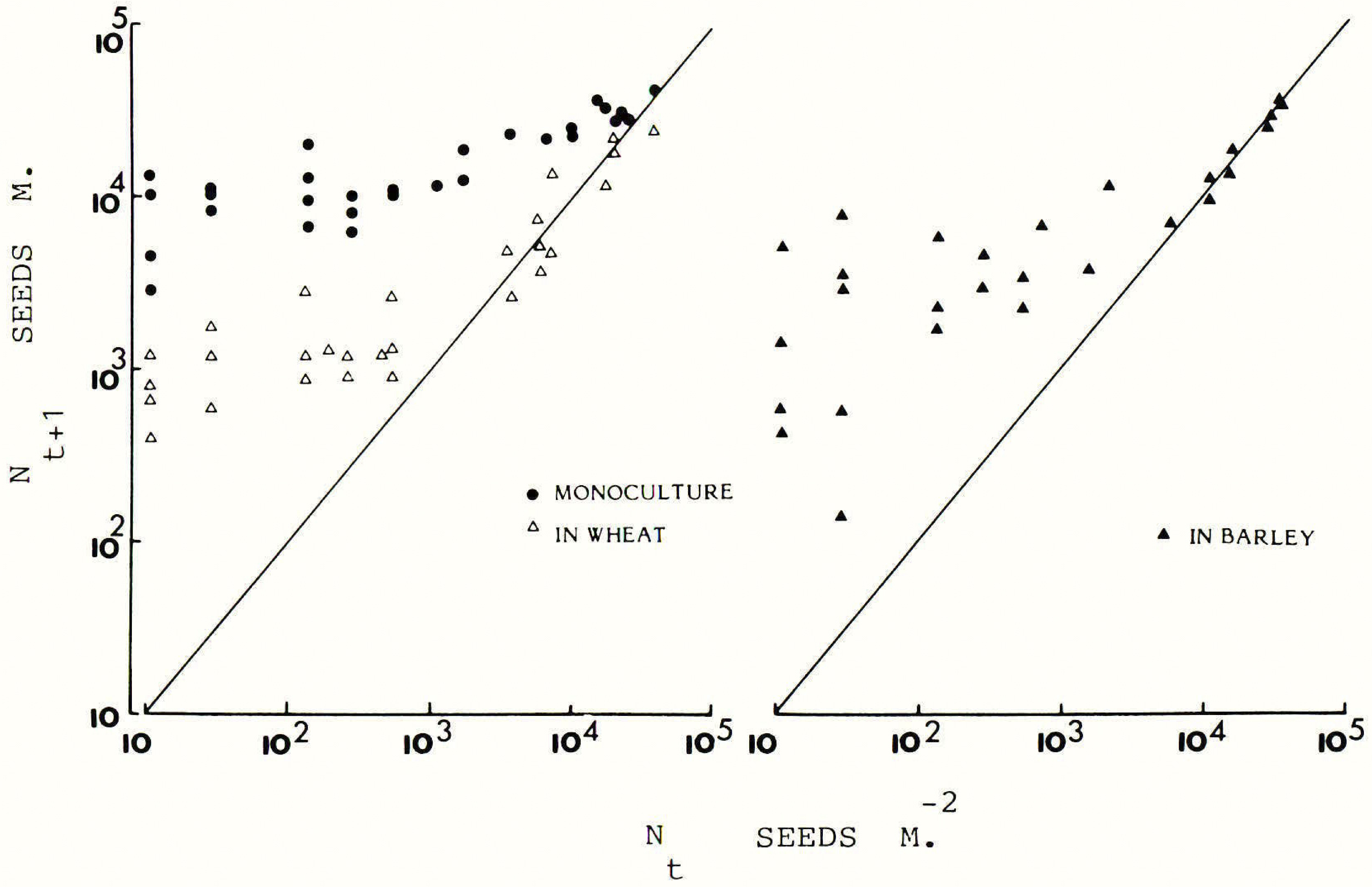
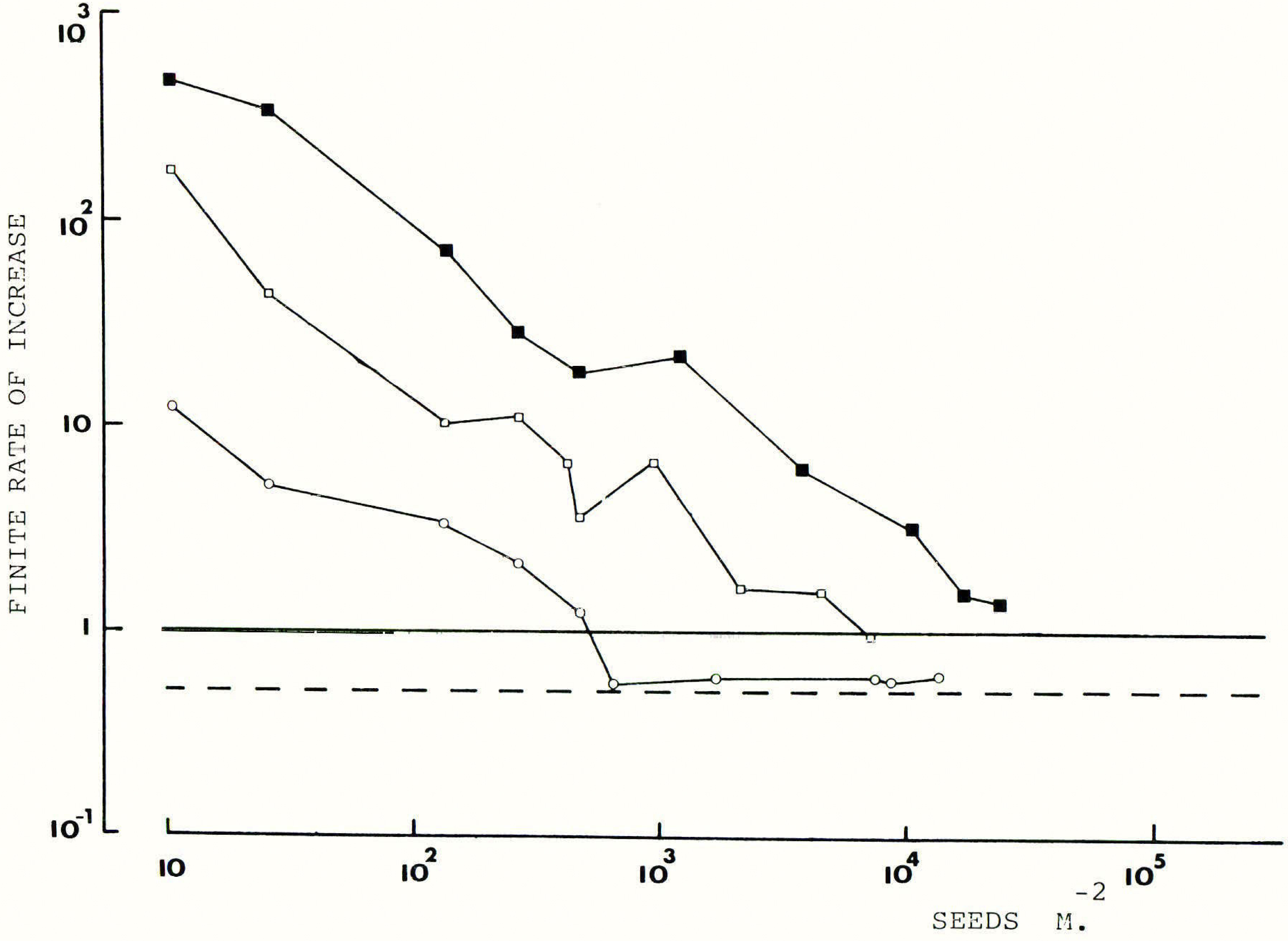


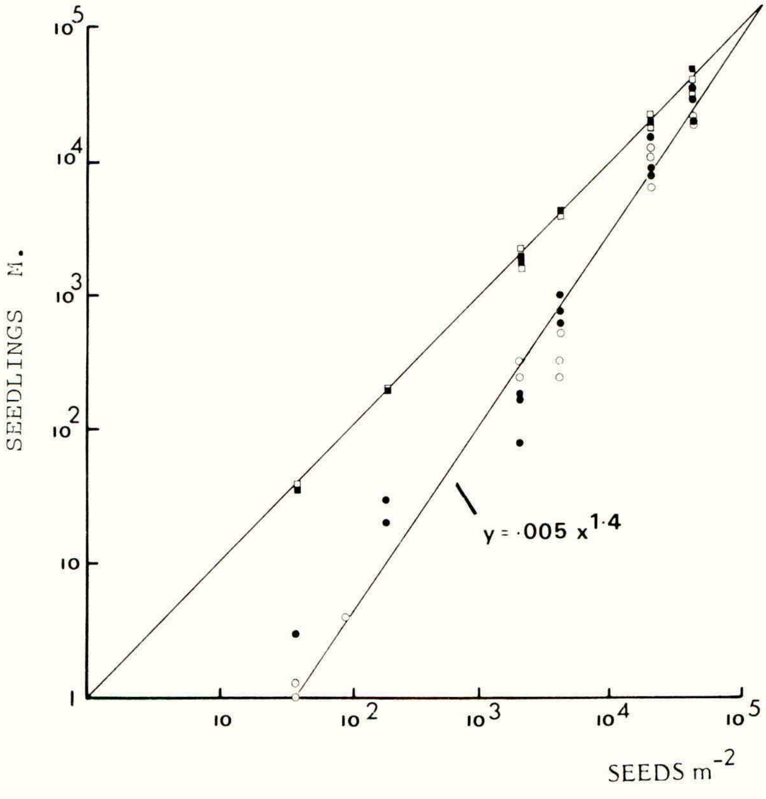
Fig. 3. Finite rates of increase of *Avena fatua* populations growing in monoculture (■), in winter wheat (□) and in winter wheat sprayed with l-flamprop-isopropyl (○). Data from Manlove,1985.



alone. This rendered a lowered equilibrium population size but one which nevertheless ensured the persistence of the weed in this trial.

Interactions between intrinsic regulatory mechanisms in populations and weed control measures may result in less straight-forward dynamics. In Bromus sterilis for instance in minimum tillage agro-ecosystems, density dependent regulation is confined over a wide range of plant densities to seed production (see details in Firbank et al. 1984,1985). Control of seedling populations by pre-emergence applications of triallate is dependent upon seed numbers on the soil surface and diminishes with increasing seed density (Fig. 4). The form

Fig. 4. The influence of triallate (applied pre-emergence as Avadex at a rate of 22.5 kg / ha) on seedling survivorship in Bromus sterilis .Circles, + triallate ; squares, control . Closed symbols B.sterilis in wheat ; open symbols B.sterilis in monoculture. The indicated power function is significant at $p < 0.001$, $R^2 = 0.923$.



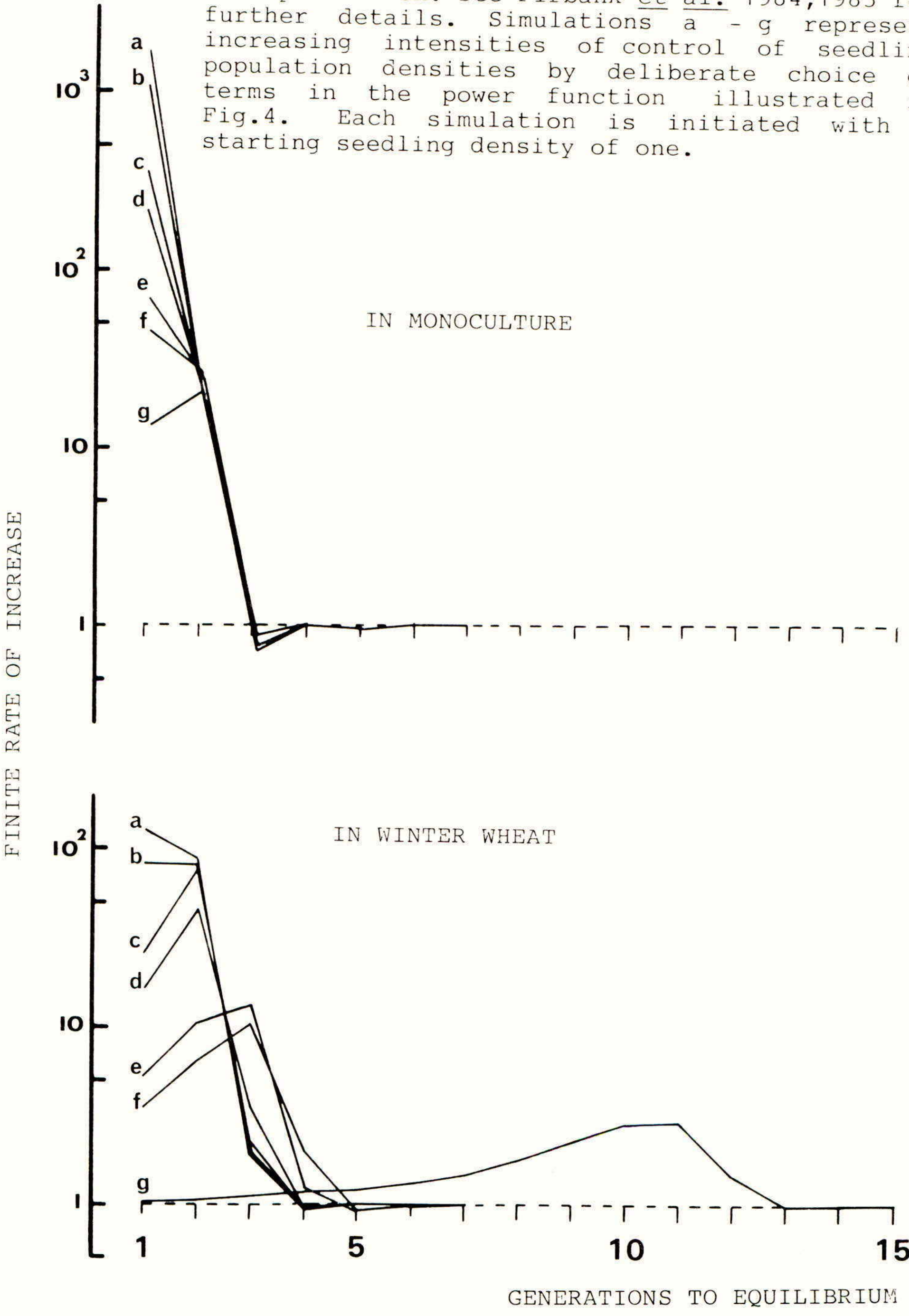
of this positive density dependence of seedling on seed numbers in the presence of triallate is a power function; the constant in the equation determines a threshold seed density necessary for the survival of a single seedling and the exponent, the approach to the locus of complete survival of seeds to seedlings.

Simulations indicate an interaction of this positive density dependent regulation with intrinsic regulation in determining the pattern of population growth rates as equilibrium populations are reached (Fig. 5). In monoculture the high seed fecundity of adult B. sterilis plants enables the population to rapidly achieve densities that nullify the influence of the herbicide. In the presence of the crop, seed production by B. sterilis is reduced and the population takes longer to achieve an equilibrium level. Moreover the pattern of approach to equilibrium is determined by the form of the seedling survivorship function. As the degree of control is increased more generations of the population are required to 'step up' the seedling survivorship curve. Initially populations at relatively low densities, experience low intra-specific regulation of seed production and population growth rates rise (simulations c - f). Subsequent populations reach sizes when seed production is strongly regulated and population growth rates fall. Thus a control regime and its density dependence interacting with natural regulation in B.sterilis yields a complex and not easily perceived pattern of growth rates.

CONCLUDING REMARKS

A weed species is inevitably recognised as intractable if under weed management, it persists at a level of abundance which either causes crop damage or will do so immediately control is relaxed. If correct this recognition is based on the ecological knowledge that the species has a high population growth rate and that currently available control measures are insufficient to contain populations at non-injurious levels. Comprehending the reason for this insufficiency requires an appreciation of the way in which weed control measures act in determining population trajectories. Where the efficacy of a control measure is itself dependent on the weed population density, it is crucial to know the precise nature of this relationship and the determinants of fitness in the weed population. Both control measures discussed earlier for A. fatua and B. sterilis achieve a lowering of population growth rate given particular biotic characteristics of the agro-ecosystem in which they are deployed. Density dependent interactions in themselves are therefore hardly surprising and can be harnessed to good effect as in the case of A. fatua. Moreover it is probable that in other weed management systems dependent on a limited number of herbicides, density dependent control would be found

Fig. 5. The simulated pattern of population growth rates of *Bromus sterilis* experiencing positive density dependent regulation of seedlings and density dependent regulation of seed production. See Firbank *et al.* 1984,1985 for further details. Simulations a - g represent increasing intensities of control of seedling population densities by deliberate choice of terms in the power function illustrated in Fig.4. Each simulation is initiated with a starting seedling density of one.



if it were not for sophisticated spraying techniques for finding target weeds. The simplest explanation for a control that is density dependent is that one plant by virtue of size protects smaller individuals beneath it from receiving a lethal spray dose from above ! Moreover it is predictable that in instances where spraying technique fails to achieve recommended standards density dependence will be common. As illustrated for B. sterilis unexpected population trajectories may also occur. Such discoveries require rigorous ecological analysis but which can often be achieved by one experimental trial over a range of infestation densities.

ACKNOWLEDGEMENTS

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GROWTH PATTERNS IN CYPERUS ROTUNDUS

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ABSTRACT

A series of observations and experiments are described, in which the pattern of rhizome and tuber development are followed in pot-grown *Cyperus rotundus*. It is shown that the development of tubers with dormant apices (dormant tubers) is normally delayed until the stage of tertiary or quaternary rhizome growth but that dormancy can be induced in tubers on secondary rhizomes by restricting growth in small pots. This effect may be at least partially attributed to water and nutrient stress.

INTRODUCTION

Cyperus rotundus L. has been repeatedly cited as the world's worst weed following Holm *et al's* (1977) ranking. How such a ranking was derived and whether the title is deserved could be further discussed, but there is no doubt of the continuing and possibly increasing importance of *C. rotundus*, especially in irrigated agriculture. Yet it is notable that despite its notoriety there have been remarkably few detailed studies and descriptions of its pattern of growth. Hence the work described in this report, which attempted to define the sequence of events in rhizome and tuber/basal bulb formation and the degree of dormancy of the tubers at different stages of growth as influenced by soil, water and nutritional factors.

MATERIALS AND METHODS

All studies were conducted in glasshouses at the Weed Research Organization (WRO) near Oxford, U.K. with supplementary heating to 20-25°C and lighting for 14 h day length as required during winter months. A variety of growing media were used as described for individual studies. The plant material was in all cases a clone of *C. rotundus* ("WRO clone 1") originating from Zimbabwe and continuously cultured, vegetatively, at WRO since importation in 1958. Individual tubers were initially separated from well-established stock pots with a dense rhizome and tuber system.

In order to ascertain that the restriction imposed by conventional pots (resulting in bending of the rhizome system in a circular pattern), does not alter the general behaviour of the rhizomes and tubers, large containers were constructed comprising sheets of plywood 60 x 90 cm lined with polyethylene and separated by 1.2 cm wooden slats around the sides and bottom. These were filled with Begbroke sandy loam soil and watered from above as required. As growth patterns from these soil sandwiches were indistinguishable from those in pots, all subsequent studies were in pots.

In all studies, the complete rhizome systems were washed free of soil and diagramatically mapped, starting from the parent tuber, in such a way that the state of the tubers could be summarised for each tuber "set" according to its stage of removal from the parent, i.e. all secondary tubers/basal bulbs (borne by rhizomes from the primary shoots), all tertiary, all quaternary, etc.

A number of experiments were conducted in which fertilizer, pot size and watering regimes were varied. In these experiments there were three to six replications. 'Normal' watering involved at least daily and often twice-daily watering of pots as appeared to be required. Some more carefully controlled watering systems and other specific details are provided in the results section.

RESULTS

Sequential observations

When individual tubers are separated from a rhizome system and planted in fresh soil, the initial sprout is a vertical underground stem with scale leaves. On reaching the soil surface, further elongation is inhibited by light, leaves begin to develop at the apex and a swelling known as the basal bulb develops at a point generally about mid-way between the parent tuber and the soil surface. Within a week from emergence of the shoots, rhizomes begin to emerge from the basal bulb, from 1 up to 4 per basal bulb. The rhizomes grow horizontally forming scale leaves at intervals of 1 to 4 cm but no roots or buds are formed in the axils of these scales. The primary rhizomes may only grow a few cm before turning up to emerge and form leafy shoots with modest swellings at the base closely analagous to the basal bulbs on primary shoots. Roots develop freely at the point of the swelling and some days later one or more buds on the basal bulbs of the daughter shoots grow out to form secondary rhizomes. These rhizomes may also emerge to form leafy shoots and basal bulbs before outgrowth of lateral buds, to form tertiary rhizomes. There is, however, a gradual or rapid transition, according to conditions, to a pattern where the new rhizome (having formed about 6, very rarely less than 5 or more than 7 elongated internodes, each with a scale leaf), slows in growth, turns slightly upwards and forms a succession of closely packed internodes, at the same time swelling just behind the apex to form the characteristic tuber with the apical bud quite dormant. Each tuber has up to 10 nodes, each with a scale leaf and a viable bud, arranged in a tristichous phyllotaxy. Soon after the swelling develops, a few strong roots are produced, mainly from the lowermost surface of the tuber. When the tuber has reached full size, one or more buds grow out as horizontal rhizomes. These are always on the lowest side of the tuber and often appear to be those closest to the well-developed roots. In no case has a new rhizome bud been seen to sprout before the development of roots, though sprouting can occur within 1 or 2 days of root development.

Where the rhizome apex ceases growth completely and forms only a sharp point on the tuber, the tuber is "dormant" for the purposes of this paper. Where, as in early stages, it emerges as a shoot it will be described as "emerged". Intermediate behaviour is common where the apical bud grows out to several cm long but fails to emerge - this category is described as "active" (though some do in fact lapse into prolonged dormancy after making some growth). No distinction is made between basal bulbs and tubers. They are clearly distinct in their extreme forms but appear to intergrade quite gradually and all leafy shoots, including the primary, are regarded as "emerged" tubers.

A typical pattern of development is illustrated in Fig 1. This shows the tendency for the low-order rhizomes in the younger plant to emerge as leafy shoots while at the later stages there is greater development of 'dormant' tubers.

Such patterns can be summarised as in Fig 6, each column of the histogram representing a set of tubers starting with the primary shoots and indicating the increasing proportion of dormancy in the higher-order (later) sets of tubers. As dormant tubers only begin to be formed later there is a steady increase in the overall proportion of dormant tubers with plant age.

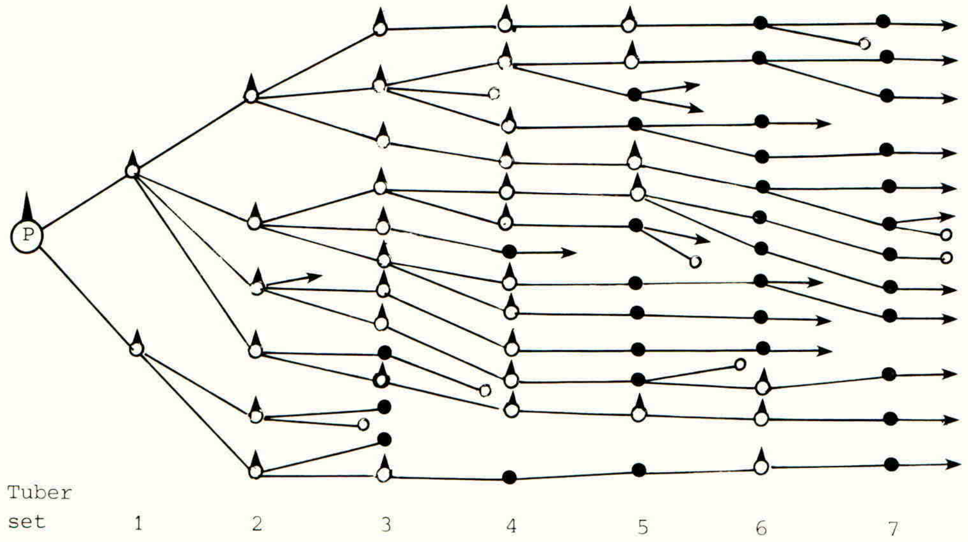

Figure 1. Diagramatic representation of the tuber system of a single plant grown with complete fertilizer in an 18 cm diameter pot. P = parent tuber: ▲ emerged or active tuber apex: ● dormant tuber: ○ immature tuber

Replicated experiments

The first replicated experiment (see Fig. 2), involving different soil types and a common level of fertilizer (John Innes base fertilizer at 7.5 g/ℓ soil) in a single (12.5 cm diameter) pot size showed a range of final tuber numbers according to soil type (most in peat, least in clay soil) and increasing levels of dormancy with increasing total tuber number, as expected from the description above. No soil type particularly favoured the production of dormant tubers.

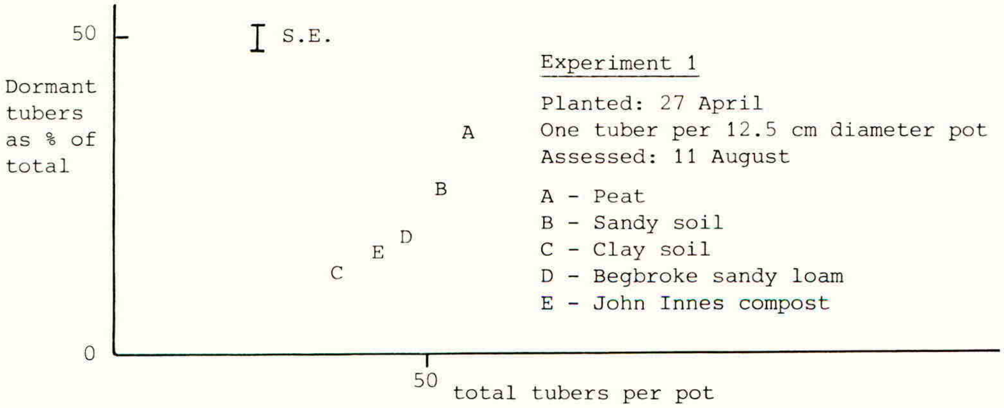

Figure 2. Relationship of dormant to total tubers as affected by soil type.

The next experiment again used a common level of fertilizer (John Innes base at 10 g/ℓ soil) but varied pot size, and from Fig. 3 it is clear that small pots (7 cm diameter) greatly favoured the production of dormant tubers.

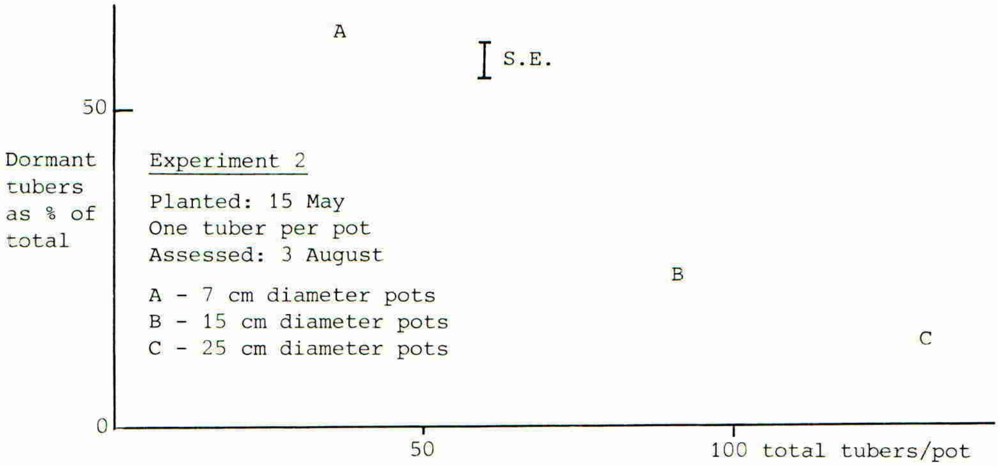

Figure 3. Relationship of dormant to total tubers as affected by pot size.

A third experiment (Fig. 4), fertilizer as experiment 1, in which there were differing numbers of tubers sown per pot, once more confirmed that pot size had a very marked influence on dormancy.

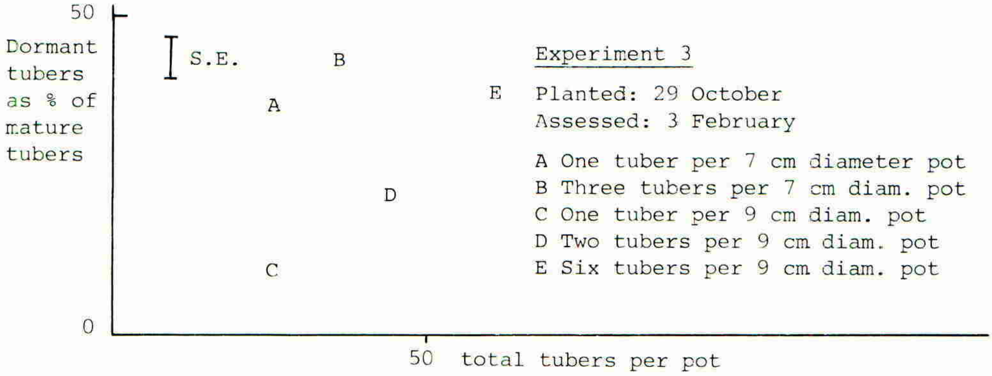

Figure 4. Relationship of dormant to total mature tubers as affected by pot size and number planted per pot.

A larger experiment was then conducted involving 3 pot sizes, and 6 fertilizer treatments. Basic P (2.4 g P_2O_5/ℓ) and K (1.2 g K_2O/ℓ) were not varied but N was applied at 3 levels of 0.23, 0.46 and 0.91 g N/ℓ as "Nitroform". Fig. 5 shows that there was again an effect of pot size (only the two extreme sizes are illustrated) which was not greatly influenced by the addition of fertilizer. For instance, treatments e and f in small pots produced very nearly the same tuber totals as in the unfertilized large pots, but there was still a distinctly higher level of dormancy. Analysis of the patterns of growth in more detail (Fig. 6) shows that the higher level of

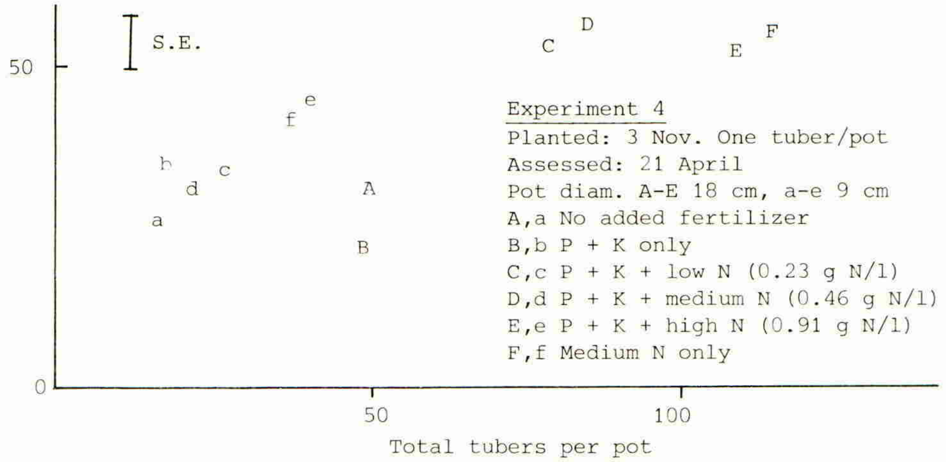

Figure 5. Relationship of dormant to total mature tubers as affected by pot size and fertilizer addition.

dormancy in the smaller pots (mean of all fertilizer treatments) is not so much due to greater dormancy levels in the lower-order tuber sets but to a reduction in the number of daughter rhizomes (branching factor) in the early stages which minimised the total tuber numbers in the lower-order, less dormant sets.

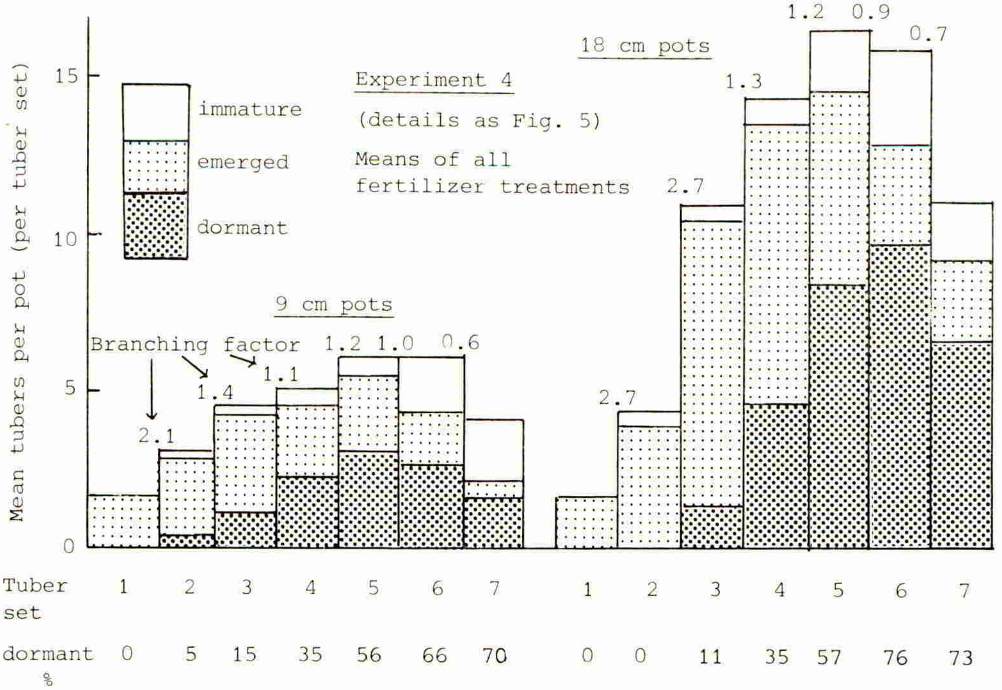

Figure 6. Distribution of dormant, emerged and immature tubers and % dormancy, by tuber set (1 = primary shoots, 2 = secondary shoots/tubers etc).

A further experiment with pot sizes and fertilizer again showed little influence of fertilizer in two of the three pot sizes, though some effect was apparent in the intermediate (9 cm diameter) size (Fig. 7). Liquid feeding involved the use of a proprietary "Vitafeed 102" containing N, K and trace elements. Weekly additions to 7 cm diameter pots were equivalent to 1.8 mg N and 3.6 mg K_2O per pot initially, increasing to double these amounts after 6 weeks. For 9 cm pots quantities were double, and for 12.5 cm pots they were initially 4.5 mg N + 9 mg K_2O, increasing to 7.2 mg N + 14.4 mg K_2O after 6 weeks. In this case a more detailed analysis of patterns in the two smaller pot sizes (mean of all fertilizer levels) showed little difference in branching patterns but distinctly higher dormancy levels in the lower order tuber sets, involving the production of a considerable proportion of dormant tubers directly from the primary shoots. Sets 1 to 4 in 9 cm pots showed 0, 5, 15 and 39 % dormancy respectively while in 7 cm pots corresponding figures were 0, 24, 57 and 67%.

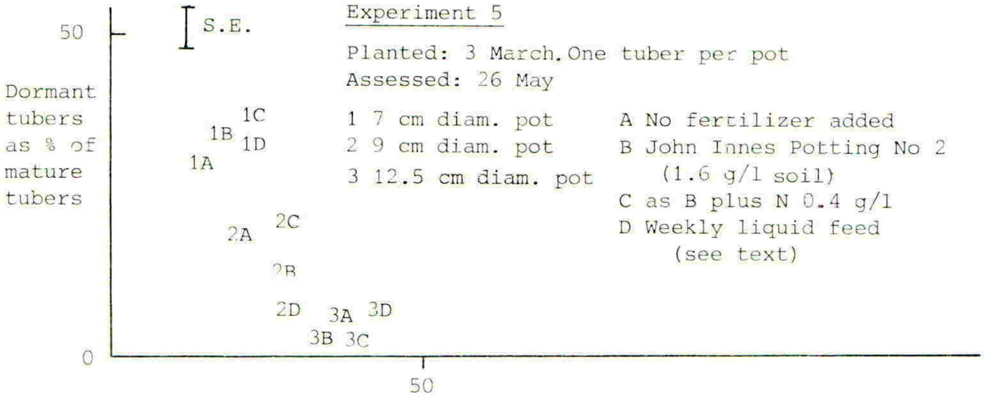

Figure 7. Relationship of dormant to total mature tubers as affected by pot size and fertilizer addition.

One further experiment in which fertilizer was varied, in a single (9 cm) pot size showed a marked influence of nutrient when applied repeatedly as a twice-weekly liquid feed (see Fig. 8).

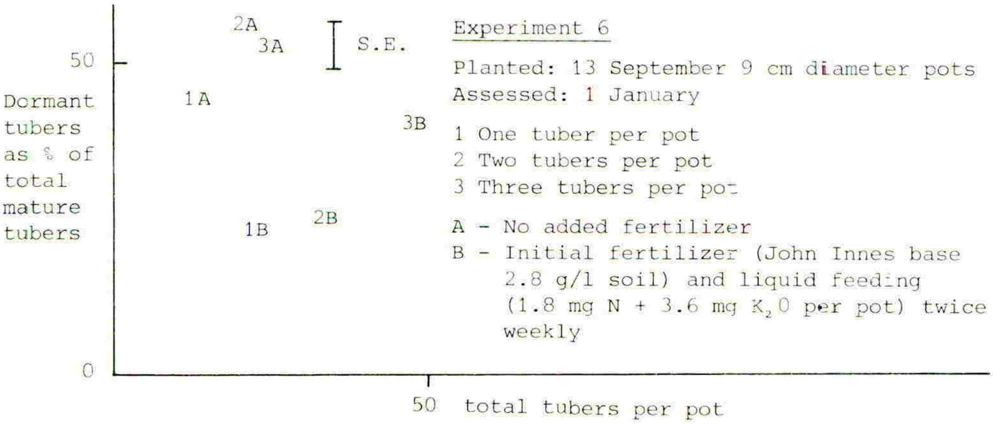

Figure 8. Relationship of dormant to total mature tubers as affected by number of tubers planted, fertilizer addition.

The next two experiments explored the possibility that greater dormancy in smaller pots might also be caused by water stress. The first, in 9 cm pots (results not presented), suggested that dormancy was not appreciably increased by reduced watering relative to "normal" but was almost eliminated under continuous moisture achieved by sub-irrigation. The second, using larger (12.5 cm diameter) pots (Fig. 9) provided evidence of some influence of reduced watering and a less marked but still significant reduction in dormancy levels under sub-irrigation.

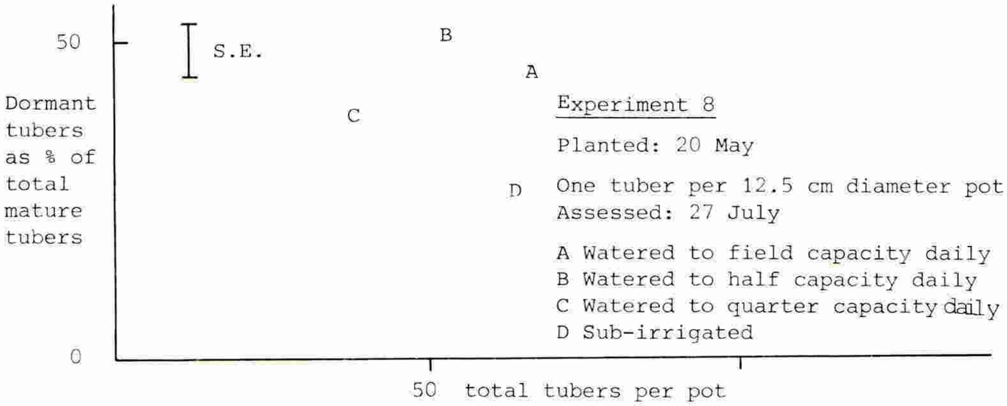

Figure 9. Relationship of dormant to total mature tubers as affected by watering regime.

DISCUSSION

Observations on sequential growth have posed a number of interesting areas for further study. Firstly there is the limited number of sprouts growing out per tuber which is analagous to the behaviour of 7-node fragments of *Elymus (Agropyron) repens* studied by Chancellor (1968). There is clearly a correlative inhibition imposed by the first one or two buds to sprout, perhaps those nearest the original apex but this has not been studied closely. It has already been noted that this correlative inhibition is overcome by cytokinins (Parker & Dean, 1972).

The number of buds on the "basal bulb" of primary shoots has not been studied but it appears likely that the number of secondary rhizomes growing out is also controlled by some correlative inhibition. The growth of the rhizome and the reason for its strictly finite development before turning up and emerging or forming a tuber also deserves further analysis. It is notable, in particular, that the number of nodes is much less variable than the length, and it is possible that the change in behaviour of the apex results from a change in ratio between different growth substances, or between growth substances and nutrients reaching the apex, which could presumably result from selective restriction of movement through the nodes.

The mechanism regulating the behaviour of the apical bud of the rhizome has not been explained but the series of experiments reported above show that it is very strikingly influenced by environmental conditions. The plant may go on to produce 100 or more tubers and basal bulbs with very few rhizome apices remaining dormant in the form of 'dormant' tubers (as in 25 cm pots in Fig. 3). Conversely, in very constricted conditions in small pots, dormant tubers may be produced directly from the primary shoots.

The influence of the constricted conditions in small pots could be attributed to limited nutrition, but several of the experiments failed to confirm any clear influence of fertilizer regime. Only where nutrient was provided continually by liquid feed was the tendency to dormancy in small-pot conditions clearly overcome (Fig 8)

Similarly, in spite of regular watering, there could have been greater moisture stress in small pots, and limiting the water availability to below field capacity did, in two of the three experiments tend to increase dormancy, though not to the same extent as restricted soil volume. Continuous wetness reduced the production of dormant tubers.

Both moisture stress and nutrient (especially N) could be expected to affect the balance between cytokinins and inhibitors such as abscisic acid, in a way that could explain the varying dormancy to some extent, but there is still the question of how the apical bud of the tuber is caused to be dormant, yet lateral buds are not inhibited from growing out as rhizomes.

Although the mechanisms have not been clearly resolved, this study demonstrates that the dormancy of *C. rotundus* tuber systems is profoundly influenced by the density of the population per unit volume of soil, and illustrates ways in which the phenomenon can be analysed and illustrated. Further study could provide insight into the mechanisms and hence improved understanding of the way in which the shoot and tuber populations of this important weed are self-regulated.

ACKNOWLEDGEMENTS

I wish to acknowledge that much of the detailed work involved in this study was conducted by Mr G G Hawkins, Mr M L Dean and Miss N Pattison. The project was funded by H.M. Overseas Development Administration.

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POPULATION DYNAMICS OF CYPERUS ESCULENTUS L. (YELLOW NUTSEDGE) IN ZIMBABWE

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ABSTRACT

The demography and spread of populations of Cyperus esculentus was examined in mono-culture in Zimbabwe. Viable seed formed but seedling establishment was infrequent. Population spread and its survival through a cool dry season depended on tuber growth. Density-dependent effects on the propagation of new ramets or of tubers per established ramet largely determined population regulation, since ramet mortality was not very density-dependent. Tubers had 3-7 buds/tuber. In undisturbed growth from 15 tubers/m^2, tuber mortality was 0.03 tubers/0.1 yr and tuber formation occurred rapidly reaching the carrying capacity of the habitat (10,400 tubers/m^2) within two seasons. With regular and effective removal of ramets tuber mortality was 0.18 tubers/0.1 yr. A population dynamics model fitted to these data predicted variations in population structure over several seasons and a range of conditions. The results are discussed in relation to control strategies for this weed.

INTRODUCTION

Worldwide, Cyperus esculentus (yellow nutsedge) is considered one of the worlds' worst weeds (Holm et al, 1977). In the last two decades it has become a major weed problem in Zimbabwe; by 1980 for example, 64 per cent of herbicides used in tobacco were specifically for the control of C. esculentus nutsedge (Cousions, 1981). In the United States the weed is the most troublesome perennial in the Corn Belt despite the use of control practices which usually prevent loss of crop yields (Stoller, 1981).

Sagar & Mortimer (1976) suggested that studying the demography of such persistent weeds would provide more understanding of the factors regulating their populations than studies of particular phases or interphases of their life-cycle. Demographic studies can identify those characteristics which regulate the proliferation and persistance of weed populations. Also, from demographic studies it is possible to construct mathematical models of the life-cycle of the weed (Mortimer et al, 1978). This paper describes how density-dependent factors regulate populations of pure stands of C. esculentus and discusses the potential uses of a model, derived from the demographic data, it evaluating weed control strategies.

The life-cycle of C. esculentus is presented in a flow diagram form in Figure 1. Six "age-states" (Rabotnov, 1969) are distinguished in the life-cycle along with the flux of individuals from one state to another with the passage of time. The aerial fraction is subdivided into pre-reproductive plants or ramets (seedlings and immature plants arising from tubers) and reproductive or adult ramets (flowering or non-flowering). Adult ramets can produce several rhizomes whose apices may either differentiate into new

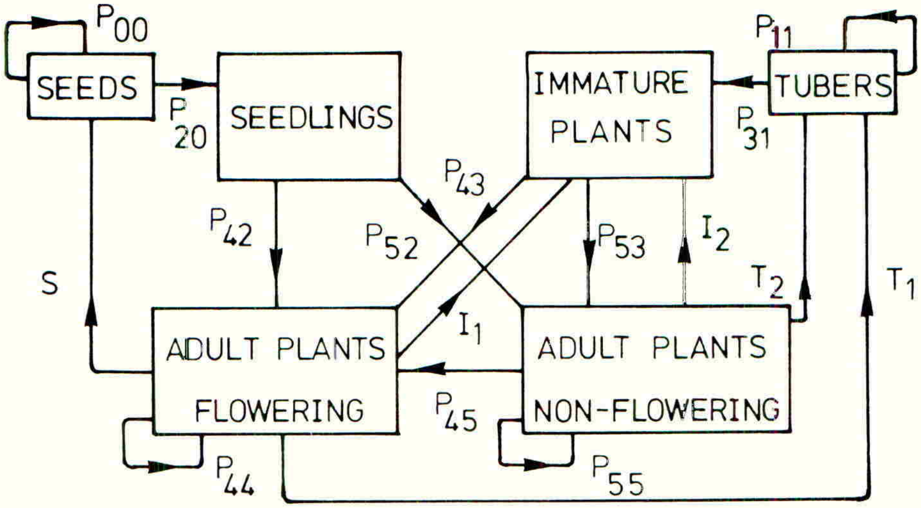


Fig. 1. Flow diagram describing the life cycle of *C. esculentus*. The demographic events taking place in any one time period are:-

Transition Probabilities

P00 - seed survival
P20 - seed germinating
P11 - tuber survival
P31 - tuber sprouting
P42 - seedling becoming flowering adult
P52 - seedling becoming non-flowering adult
P43 - immature plants becoming flowering adult
P53 - immature plants becoming non-flowering adult
P44 - flowering adult survival
P45 - non-flowering adult flowering
P55 - non-flowering adult survival

Fecundities

S - number of seed produced per flowering adult
T_1 - number of tubers produced per flowering adult
T_2 - number of tubers produced per nom-flowering adult
I_1 - number of immature plants per flowering adult
I_2 - number of immature plants per non-flowering adult

These probabilities and fecundities constitute the elements of the transition matrix of the model described in Fig. 5.

ramets or tubers. The rhizomatous growth habit also enables the weed to spread.

In Zimbabwe the rainy season is from November to March and growth and spread of the weed occurs mainly during this period. Very little if any rain falls from April until October and by the end of the dry season all individuals of the aerial fraction of the population have usually died. New growth is subsequently initiated from seed or tubers with the onset of the rains.

MATERIALS AND METHODS

The *C. esculentus* material studied was shown to be typical of several other clones in general growth characteristics (Lapham 1985).

Intraspecific competition and density-dependent processes in the life-cycle of *C. esculentus* were measured during growth of the weed from a range of tuber densities, at Kutsaga Research Station, Harare, Zimbabwe. Sprouted tubers were planted in plots of 1.5m x 1m on 4 August 1983 and measurements of growth continued until 2 August 1984. Original tuber densities were 5, 15 117, 1500 and 10,000/m^2. The births and deaths of aerial shoots (ie ramets) were assessed on 10 occasions from 10 October 1983 until 2 August 1984, in permanent quadrats 0.3m x 0.3m. In each plot quadrat newly emerged ramets were tagged with different coloured wires to facilitate their later identification. On 5 of the occasions further quadrats (0.3m x 0.3m) within each of the plots were excavated to a depth of 0.2m and the total number of tubers recovered and counted.

Newly emerged ramets at each assessment were classified as immature until the next assessment date when they were classified as mature adult ramets. The average number of new ramets produced per adult plant during the period between assessments was estimated by dividing the number of newly emerged plants during the period by the total number of living adult plants present. The production of tubers by adult plants was similarly estimated from the number of new tubers present in the destructively sampled quadrats divided by the total number of living adult plants in the permanent quadrats. Comparison between various density-dependent processes at different original tuber densities, was made by comparing their k-values. The k-values are the logarithm of the value of any of the density-dependent attributes at the lower density (1 tuber/m^2) divided by its value at each of the higher original tuber densities (eg. Fig. 2).

The spread and propagation of the weed from a single tuber was monitored from November 1979 to August 1981. A sprouted tuber was planted in the centre of 30 plots each 6m x 6m. The radius of growth of the weed from its origin to the periphery was measured on 18 occasions. The number of new tubers produced were estimated by excavating 2 sample areas on 13 occasions. The survival of buried tubers of known viability was monitored in two experiments. In the first experiment ramets produced by the tubers were removed within 2-3 weeks before they became mature: this was known from preliminary experiments to prevent the production of new tubers. Samples of the planted tubers established in July 1982 were recovered at about 6 month intervals until May 1984, and their viability assessed. In a second experiment tubers were planted in November 1983 and the population was allowed to grow undisturbed; 3 and 6 months later the planted tubers were recovered and their viability was assessed. In each of these experiments 15 tubers/m^2 were planted and their location was marked by placing a coloured wire down the hole they were planted in. They were recovered by tracing the wire from the soil surface to the tuber, at each sampling.

RESULTS AND DISCUSSION

In these rain-fed conditions in Zimbabwe seedling recruitment played an insignificant role in the fluctuation of *C. esculentus* populations. In terms of Fig. 1, the probability of a seedling becoming an adult, was extremely small ($P42 + P52 < 3 \times 10^{-4}$; Lapham, 1985). Tubers were the survival units which persisted between rainy seasons. Fluctuations in tuber numbers were thus a reflection of tuber longevity and changes in the mortalities and

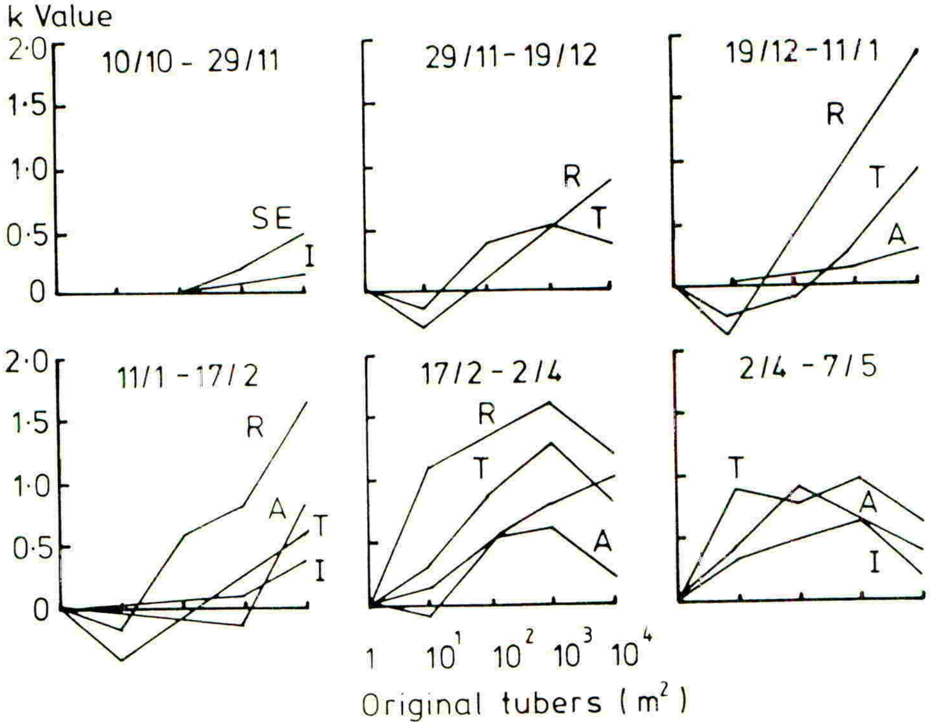
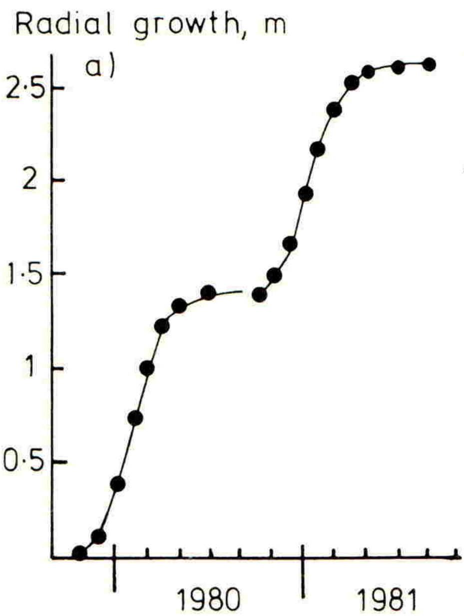


Fig. 2. The effect of competition arising from a range of original tuber densities on the k values of attributes regulating the population structure of C. esculentus from 10/10/83 to 7/5/84; k value are the logarithm of attributes measured at 1 tuber $1m^2$/attribute measured at other populations. Attributes measured were SE = sprout emergence from planted tubers, I = immature plant mortality, A = adult plant mortality, R = new ramet production per adult ramet, and T = new tuber production per adult ramet.

fecundities of all ramets of the aerial fraction of the population.

The dependence of life-cycle processes on the planting density of the original tubers is depicted in Figure 2, from 10 October 1983 to 7 May 1984, the main period of weed growth. From 29 November to 17 February the vegetative reproductive processes of new ramets (R) and, to a lesser extent, tuber production by adult plants (T), were clearly density-dependent. The survival of immature (I) and adult ramets (A) were largely unaffected by competition except at the highest density (10000 tubers/m^2), (ie k values were close to zero). After 17 February up to 7 May increasingly unfavourable dry and hot conditions decreased the fecundity and survival of ramets at all densities but not on a pattern consistently related to tuber density, particularly over the range from 15 to 10000 original tubers/m^2.

The density-dependent characteristics of the C. esculentus life-cycle enables populations to expand rapidly in uncompetitive conditions as demonstrated by the unrestricted growth from a single plant, which spread 2.5m radially (Fig. 3a) and produced over 150,000 new tubers in 2 years (Fig. 3b). This characteristic of the weed is of great importance in the expansion and proliferation of new infestations in arable land particularly



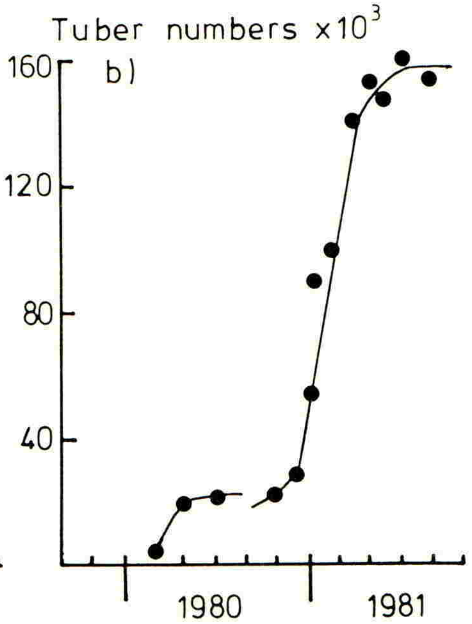


Fig. 3a. The relationship between radial growth of a single plant (y) and time (x) for two seasons, i) 1 Nov 79-80 Sept 1980 and ii) 30 Sept 1980 - 30 June 1981. In i) $y - S_1 = 1.41$ (ie $-0.081x^2$) and in ii) $y - S_2 = 1.22$ (ie $-0.071x^2$) $S_1 = 0$ and $S_2 = 1.38$ are radii at the start of growth in each season.

Fig. 3b. The relationship between the number of tubers produced by growth from a single original plant (y) and time (x) for two seasons i) 1 Nov 1979 to 30 June 1980 and ii) 1 June 1980 to 31 July 1981. In i), $y - t = 1/(0.0000571 + 3.6 (1.9x)$ and ii), $y - t_2 = 1/(0.00000741 + 1.19 (8.5x)$. $t_1 = 0$ and $t_2 = 16983$ and are the number of tubers on 1 November 1979 or June 1980 respectively).

after cultivation and before establishment of the crop. In densely competitive conditions, on the other hand, the marked density-dependence of the propagation of new ramets and tubers prevents over-populating an already crowded habitat, reflected in the lack of density-dependent mortality of ramets in Fig. 2. It is apparent that combining these density-dependent processes of the life-cycle would result in attaining a population which reaches a maximum level, or carrying capacity for the habitat, with time. This would be reflected here by a maximum density of tubers since it is this fraction of the population which survives adverse conditions. Maintenance of the tuber population at or about the carrying capacity would depend upon the formation of new tubers equalling losses from the number of viable tubers. Thus at the carrying capacity of a habitat, the population growth rate, λ, would equal one.

Loss of planted tuber viability was found to be largely dependent on the continuing attachment of the tubers to the ramets that they produced. If ramets were removed at regular intervals before becoming mature, a situation comparable to frequent cultivation or chemical control with paraquat in practical situations, the surviving planted tubers lost their viability at a

TRANSITION MATRIX

$$[Nt] = \begin{bmatrix} P_{00} & - & P_{20} & - & S & - \\ - & P_{11} & - & - & T_1(n) & T_2(n) \\ P_{20} & - & - & - & - & - \\ - & P_{31}(n) & - & - & I_1(n) & I_2(n) \\ - & - & P_{24} & P_{43}(n) & P_{44} & P_{45}(n) \\ - & - & P_{52} & P_{53}(n) & - & P_{55} \end{bmatrix} = [Nt+1]$$

Where the column vector of age-classes,

$$[Nt] = \begin{bmatrix} St \\ Tt \\ SLt \\ It \\ Flt \\ NFLt \end{bmatrix}$$

Fig. 4. Matrix model used for the life-cycle of *Cyperus esculentus*, where St and St+1 = number of seeds at time t and t+1, Tt and Tt+1 = number of tubers at time t and t+1, SLt and SLt+1 = number of seedlings at time t and t+1, It and It+1 = number of immature ramets at time t and t+1, FLT and FLT+1 = number of flowering adults at time t and t+1, NFLt and NFLt+1 = number of non-flowering adults at time t and t+1. (n, is the density of original tubers and (n) denotes elements of the transition matrix which are dependent on the density of original tubers. N, is the number of individuals in each age-state).

rate of 0.18 tubers/0.1yr. If the ramets were not removed the rate of loss of tuber viability was only 0.03 tubers/0.1yr. This would suggest that regular removal of ramets would effectively reduce and could possibly eradicate populations of the weed. To do this effectively is often impossible in practical and economic terms. The formulation of a weed management strategy would be a useful approach to its control. A life-cycle matrix model of the weed's growth provides a means for comparing the efficacy of various control measures and formulating a more cogent approach to control. Consruction of the model was based on the approach of Mortimer *et al* (1978) and the probabilities and fecundities during any time period derived from the data observed experimentally form the components of a square matrix, the transition matrix. Multiplication of the transition matrix by the column vector of the number of individuals in each state at one time period, gives the number of individuals present in the next time period (Fig. 4).

Simulation of tuber population growth by the model demonstrates the characteristics of *C. esculentus* populations which contribute to their

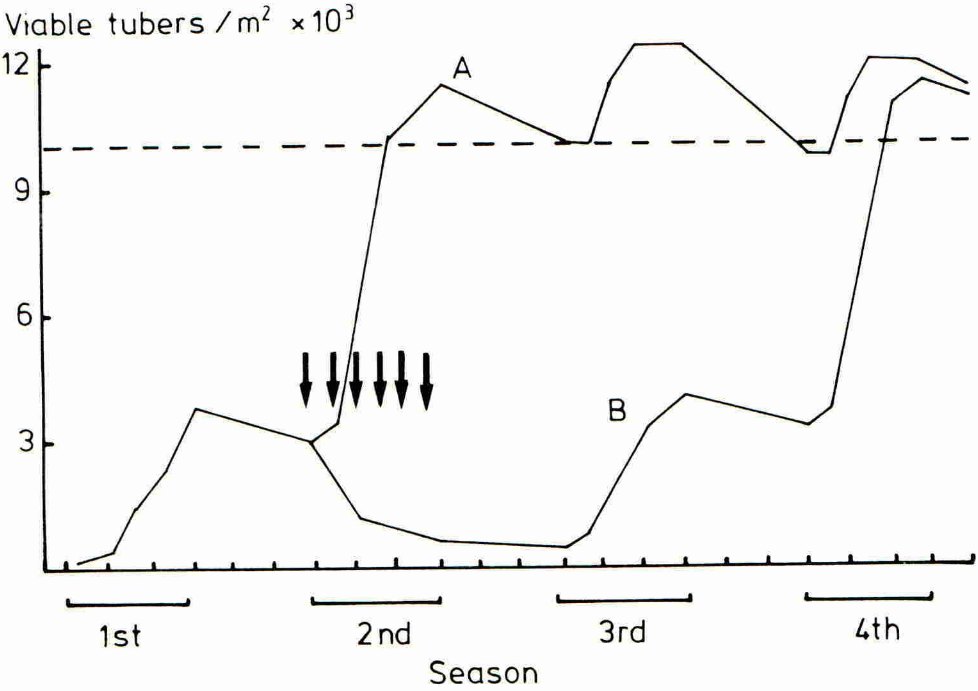


Fig. 5. Simulated changes in viable tuber numbers/m^2 growing from 15 tubers /m^2 over 4 seasons. Curve A is for undisturbed conditions with tuber mortality = 0.03 tubers/0.1yr. Curve B simulates 6 times of removal of new ramets during the second season (↓) resulting in no new tubers forming and tuber mortality = 0.18 tubers/0.1yr, with no disturbance in 3rd and 4th season. Carrying capacity, where growth rate $\lambda = 1$ is 10,400 tubers/m^2 for this habitat, shown by the dashed line.

intractable nature. Starting from 15 original tubers/m^2 tuber growth rapidly expanded and within 2 years undisturbed growth, the carrying capacity of the habitat was attained as indicated by an estimated maximum density of 10411 viable tubers/m^2 at the end of the second dry season (Fig. 5). Where production of new tubers was inhibited by early removal of all emerging ramets the loss of tuber viability increased from 0.03 to 0.18 tubers/0.1yr and the density of viable tubers decreased rapidly (Fig. 5) from over 3000 to less than 500/m^2. In the year after this control treatment, numbers of tubers increased again to more than 4000/m^2 and numbers were up to carrying capacity after one more season.

The study of the demography of C. esculentus has provided a cogent description of the life-cycle of the weed. The further use of the population matrix model has allowed an integrated synthesis of all the demographic stages of the life-cycle and indicated how the principal factors have contributed to the persistence and proliferation of the weed. Preliminary use of the model, as in Figure 4, has demonstrated its potential value in predicting how population fluctuations will occur under some different conditions. As pointed out by Mortimer et al (1980) the matrix model approach enables the investigation of various weed mangement strategies to be predicted since there is no theoretical restriction to the sequential alteration of survivorship and fecundity terms in the model in calculating rates of population changes. However, it is necessary for biological data to be acquired for a variety of management regimes before it will be possible to suggest the most practical and economic strategy for the containment or eradication of such weed populations. In this present situation, effects of crop competition, supplementary irrigation and of some current weed control practices will be studied next to provide additional biological data.

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GEOGRAPHIC SPREAD OF DATURA STRAMONIUM IN ASSOCIATION WITH SOYBEANS AND MAIZE IN ONTARIO, CANADA

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ABSTRACT

Range expansion of Datura stramonium L. northward in Ontario, Canada, is examined in relation to the length of the growing season and an increase in the hectarage devoted to the production of soybeans and maize. A model is constructed of rates of population growth under different levels of seed maturity at harvest. Geographic spread and patterns of seed production of D. stramonium in relation to climate are contrasted with those of two other weed species with expanding ranges, Abutilon theophrasti and Xanthium strumarium.

INTRODUCTION

The progressive spread northward in Ontario of large populations of a number of annual, broad-leaved weeds has been noted since at least 1974 (Shaw et al. 1974, Ontario Ministry of Agriculture and Food unpublished weed surveys 1980-1984). Herbarium records show that several of these species had been collected throughout the region since the mid-1800's. However, the recent appearance of large populations in arable fields, as opposed to sporadic occurrences in ruderal areas, suggests that their spread may be due to the availability of new habitats and/or genetic changes within the populations. Brussard (1984) has noted that the rarity of widespread species at the periphery of their ranges may result from these areas being ecologically marginal, or from the association of these species with particular habitats which are also uncommon at the periphery. Crop systems constitute very specific habitats, and the movement of a crop into a new area might be expected to encourage the simultaneous spread of associated weed species. Furthermore, Ontario is at the northern margin of the distributions of many widespread weed species in North America, and the length of the growing season, among other factors, may impose limits on the success of seed production. Differential rates of spread among these weed species are apparent. Here I examine rates of population growth and geographic spread of Datura stramonium L. in relation to the expansion of field crop production in Ontario and length of the growing season. These are contrasted with rates of spread of two other weeds with expanding ranges and similar ecological traits, Abutilon theophrasti Medic. and Xanthium strumarium L.

EXPANSION OF SOYBEAN AND MAIZE PRODUCTION IN ONTARIO

The hectarage devoted to soybeans and maize in Ontario has increased dramatically since the 1940's, due both to improved commodity prices and the introduction of short-season, pest-resistant varieties. Production was centered in the southwestern region of Ontario prior to the early 1960's, but has since spread northeastward across the Province, largely at the expense of hay and cereals (Kay and Stonehouse 1984). The most rapid increase in maize production occurred during the 1960's, whereas that of soybeans occurred during the 1970's (Table 1). During the last ten years, the hectarage of both crops in the southern part of the province has largely stabilized, while production continues to increase rapidly in Western Ontario and parts of Central and Eastern Ontario along the Great Lakes.

TABLE 1

Maize and soybean hectarages in Ontario between 1952 and 1984 in southern counties and the remainder of the Province

	1952	1962	1972	1982	1984
Maize					
Southern	116,000	150,000	312,000	400,000	467,200
Remainder	8,000	22,000	174,000	400,000	412,800
Soybeans					
Southern	67,720	88,080	160,600	322,000	339,600
Remainder	1,080	320	1,400	38,000	72,400

A number of highly effective preplant incorporated and preemergence herbicides were registered in Ontario in the 1960's and 1970's for control of broad-leaved and grass weeds in maize and soybeans. Their widespread use has allowed late-germinating, large-seeded weeds, which can escape their effects, to increase in abundance and avoid the competitive effects of other weeds. These weeds can be particularly problematic in soybeans, where few postemergence herbicides are available in Canada, and in maize-soybean rotations, where herbicide carry-over must be avoided.

WEED RANGE EXPANSION

Datura stramonium is an annual weed of tropical origin which occurs throughout much of the United States and southern parts of Ontario and Quebec (Weaver and Warwick 1984). The earliest Canadian specimen was collected in Montreal in 1821. Numerous collections were made in the late 1800's in Ontario and Quebec along the Great Lakes and the St. Lawrence Seaway. *Datura stramonium* may have been introduced as an ornamental or medicinal plant, and these early specimens were collected exclusively from gardens, waste ground, or occasionally roadsides (Weaver and Warwick 1984). It was not recorded as a weed of arable land until the late 1950's, although it was increasingly associated with barnyards and pig farms. In the early 1970's, it was recognized as a weed of field crops in four counties of southwestern Ontario. In the next fourteen years, it spread to 25 counties (Table 2).

For comparison, the spread of *A. theophrasti* and *X. strumarium* are also shown in Table 2. *Abutilon theophrasti* was introduced to North America from Asia as a fibre crop in the 1700's (Spencer 1984). Its history and economic impact in the United States have been reviewed by Spencer (1984) and its distribution in Canada and genecological variation by Warwick and Black (in press). First recorded in Ontario c. 1860, its range expansion began earlier and has proceeded more rapidly than that of D. stramonium (Table 2). Xanthium strumarium is also an annual weed of tropical origin which has become a major weed in the United States (Weaver and Lechowitz 1983). It has been collected in Ontario since 1862 along streams, lakes or roadsides, but began to appear as a minor weed of soybeans in the southwestern part of the province in the early 1970's, and has since increased in abundance and spread to at least twenty counties (Table 2).

TABLE 2

The number of counties in Ontario for which D. stramonium, A. theophrasti and X. strumarium have been reported as weeds of soybean or maize fields between 1970 and 1984.

Year	D. stramonium	A. theophrasti	X. strumarium
1970	4	7	4
1980	7	15	5
1981	13	32	11
1982	17	34	12
1983	20	37	14
1984	25	38	20

Data are assembled from unpublished weed surveys conducted by the Ontario Ministry of Agriculture and Food and Agriculture Canada.

SEED PRODUCTION PATTERNS IN RELATION TO CLIMATE

A pronounced gradient in the length of the growing season extends through the field crop production area of southern Ontario, variably modified by the proximity of the Great Lakes (Brown et al. 1980). From 42 N 83 W in the extreme southwest to 45 N 74 W in the northeast, the mean number of frost-free days declines from 170 to 130 and the mean number of growing degree-days above 6 C from 2400 to 1780 (Fig. 1). The average date of the first killing frost in the autumn varies from October 20 in the southwest to September 25 in the Northeast. The end of the growing season for weeds of field crops may also be imposed by the date of harvest, if it should occur before frost. Maize harvest is likely to follow frost throughout most of Ontario, while soybean harvest may precede it, at least in the southwestern region of the province.

Datura stramonium initiates flowering after the formation of the sixth to eighth leaf primordium, generally in mid-July in southern Ontario. It has an indeterminate growth habit and produces a flower in the fork of each branch. Flower and seed production proceed until frost and are proportional to plant dry weight (Weaver and Warwick 1984). The fruits are large spiny capsules which contain up to 800 flat, black seeds that mature slowly over a period of 30 days after fertilization. After another 20 days, the capsules open along 4 valves to release the seeds. Immature capsules can continue to ripen in the field when severed from the parent plant, but not after exposure to a hard frost. Average percent maturity of seed capsules of D. stramonium in southwestern Ontario at the time of the first killing frost was 66% over a three-year period (Weaver, in press). However, occasional early frosts may eliminate seed production altogether. Mature seeds have a hard, impermeable seed coat and can remain viable in the soil for long periods of time (Toole and Brown 1946).

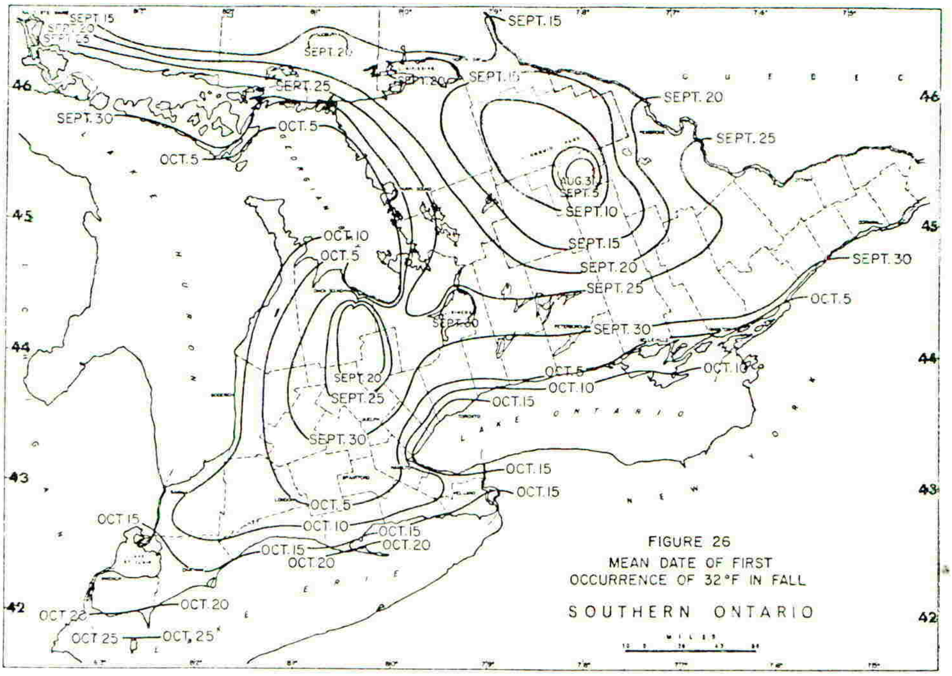

Fig. 1. Mean dates of first occurrence of frost (0°C) in the autumn in southern Ontario.

The continued spread northward of D. stramonium in Ontario will depend upon its ability to produce mature seeds in sufficient quantity to maintain population growth and dispersal. Baker (1965) has suggested that colonizing weeds may go through a "lag phase" following introduction to a new area, during which an "infective" propagule density must be built up. Similarly, Auld and Coote (1981) have argued that the rate of geographic spread of weed species is proportional to annual rates of population growth and particularly seed production.

A model was constructed to examine the way in which population growth of *D. stramonium* varies with percent seed maturity. The following parameters used in the model were derived from field experiments with natural populations of *D. stramonium* in a soybean crop in southwestern Ontario (reported in Weaver, in press):

1. Seed production per square metre is a log-linear function of plant density ($Y = 3220 \ln(x) + 2512$). At densities below 0.5 plants per square metre, $Y = 2512 (x)$.
2. Annual seed survival is 80% of the seed pool.
3. Annual emergence is 10% of the seed pool.
4. Mortality between seedling emergence and seed production is density-dependent ($Y = -5.7 + 0.6 x$) where Y is final density and x is initial density. At densities below 10 plants per square metre, there is a 20% density-independent mortality due to weather, etc.
5. Application of soil-applied, preemergence herbicides impose another 50% mortality on the fraction of the seed pool which germinates. Postemergence herbicides are not considered in the model.
6. Return of viable seeds to the soil is primarily a function of seed maturity. Four levels of seed maturity are assumed in the model to correspond to decreasing length of the growing season: 0.75, 0.50, 0.25, and 0.05 of the number of seeds produced. Dispersal is insignificant until saturating densities of seeds in the soil have been reached.

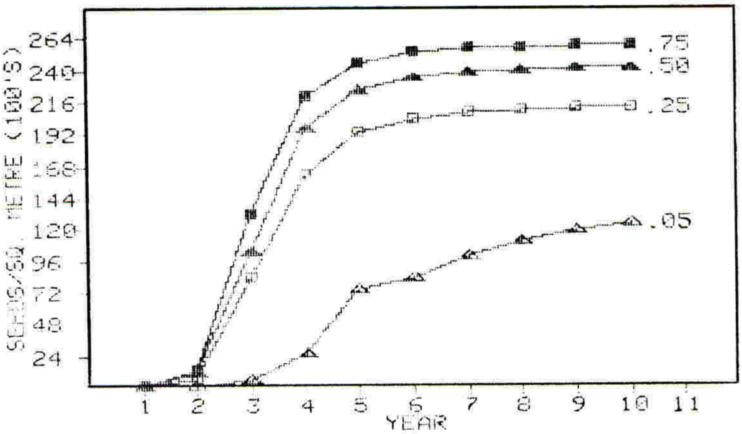

Fig. 2. Results of the model showing seed production by *D. stramonium* over time under four levels of seed maturity: 0.75, 0.50, 0.25 and 0.05.

The model was tested with starting values of 0.01 plants/m and no buried seed population. Plant density and seed production per m were followed over a 10-year period. Results of the model (Fig. 2) suggest that, in the absence of control by postemergence herbicides, populations of *D. stramonium* can build up saturating levels of seeds in the soil within 5 to 6 years of introduction to a field at all but the lowest level of seed maturity (5% of seed production). However, a 25% level of seed maturity is not reached until over 18 weeks after emergence

(September 23) even in the southwestern part of the province, and frost can occur prior to this time (Fig. 3). While parameters used in the model were based upon growth in southwestern Ontario, most would not be expected to change significantly over the latitudinal range considered.

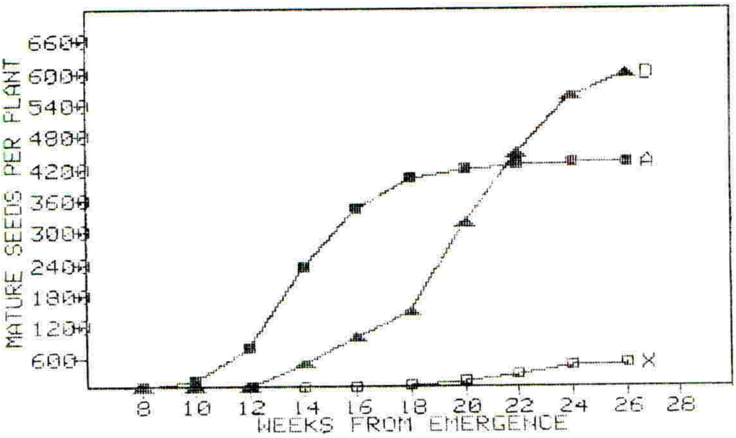

Fig. 3. Mean number of mature seeds per plant produced over the growing season in southwestern Ontario by *D. stramonium* (D), *A. theophrasti* (A), and *X. strumarium* (X).

In contrast, flowering is triggered by decreasing photoperiod in both *A. theophrasti* and *X. strumarium*, and vegetative growth all but ceases after floral induction (Oliver 1979, Weaver and Lechowicz 1982). Furthermore, they have smaller fruits, each of which contain fewer seeds and are able to mature more quickly than the large capsules of *D. stramonium* (Table 3). In southwestern Ontario, *A. theophrasti* generally begins to flower in mid-July. Its seeds mature in late August and early September and the plants often senesce completely before frost (Shaw et al. 1974). Andersen et al. (1985) found that accessions of *A. theophrasti* from a wide latitudinal range in the United States could successfully mature their seeds before frost when grown at the northern margin of their range, although southern accessions matured more slowly. They concluded that the distribution of *A. theophrasti* was not strongly controlled by photoperiod. *Xanthium strumarium* does not begin to flower until mid-August and its fruits are not mature until mid- to late-September. While vegetative parts of the plant will often senesce before frost in southwestern Ontario, fruit maturation can be prevented by early frosts. Because floral initiation is controlled by photoperiod in both *A. theophrasti* and *X. strumarium*, delayed emergence results in smaller, less competitive plants which produce fewer seeds but are still able to reach maturity (Oliver 1979, Andersen et al. 1985). Plants of *D. stramonium*, on the other hand, respond to delayed emergence with delayed flowering and a corresponding delay in seed maturation (Weaver, in press).

TABLE 3

Seed and flowering characteristics of *D. stramonium*, *A. theophrasti*, and *X. strumarium* in southwestern Ontario

Character	*D. stramonium*	*A. theophrasti*	*X. strumarium*
Weight/seed (mg)	9	10	55
No. seeds/fruit	500	35	2
Control of floral induction	growth stage	photoperiod	photoperiod
Date of flowering	mid-July	early July	mid-August
Days from anthesis to maturity	30	17	25
% seed maturity at harvest	66	100	88

GENETIC VARIATION IN RELATION TO CLIMATE

Morphological and phenological differentiation among populations of *D. stramonium*, *A. theophrasti* and *X. strumarium* has been found at the northern end of their range (Weaver et al. 1985, Warwick and Black in press, Ray and Alexander 1966, and Anderson et al. 1985). Weaver et al. (1985) found an increase in seed weight and a decline in the number of days from emergence to anthesis with decreasing length of the growing season in populations of *D. stramonium* collected along a latitudinal gradient ranging from southern Ohio through parts of Ontario. Populations of *X. strumarium*, collected from the southern United States through southern Canada, show a decrease with increasing latitute in the critical night length required for floral induction (Ray and Alexander 1966, Weaver and Lechowicz 1982). In contrast, Warwick and Black (in press) found no differentiation in time of flowering among populations of *A. theophrasti* collected from southern Ohio through Ontario, but an increase in the number of seeds produced and a decrease in weight per seed with decreasing numbers of degree-days. Evidence presented here and elseswhere would suggest that selection for early seed maturation is much stronger in *D. stramonium* and *X. strumarium* than in *A. theophrasti* (Andersen et al. 1985, Weaver and Lechowicz 1982). Electrophoretic studies have shown little evidence for allozyme variation among widespread populations of *A. theophrasti* or *X. strumarium* (Warwick and Black in press, Moran and Marshall 1978). Warwick (1985) has suggested that the apparent discrepancy between population differentiation in morphological and phenological characters on the one hand, and allozyme uniformity on the other, represents a recent divergence not yet reflected in non-selected allozyme characters.

Future geographic spread northward in Ontario of *D. stramonium*, *A. theophrasti*, and *X. strumarium* will be based upon known genetic variation in northern populations. Despite a similarity among the three species in a number of ecological traits, they may be subject to somewhat different selection pressures. The indeterminate growth habit of *D. stramonium* and the way in which it packages its seeds make it particularly vulnerable to early frosts, whereas delayed planting and long photoperiods are more likely to limit the spread of the other two species.

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VARIATIONS IN THE TOLERANCE OF GALIUM APARINE (CLEAVERS) AND STELLARIA MEDIA (CHICKWEED) TO MECOPROP

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ABSTRACT

The activity of mecoprop against ten populations of *Galium aparine* (cleavers) and three populations of *Stellaria media* (chickweed) was studied in four greenhouse experiments. There were only small variations in the response of the ten populations of *G. aparine* despite their varied origins. However, two populations of *S. media* were clearly more resistant to mecoprop than a standard one. The ED_{50}'s of the standard were 0.2-0.4 kg a.e./ha and those of the resistant populations were 5.6-9.5 kg a.e./ha. The resistant plants failed to show the normal epinastic response to mecoprop and only exhibited necrotic spots on the leaves. The activity of MCPA and dichlorprop was also appreciably poorer on the mecoprop resistant *S. media* populations.

INTRODUCTION

The development of ecotypes of weed species resistant to previously effective herbicides has been recorded with increasing frequency over the last 10-15 years (Lebaron & Gressel, 1982). Many of the problems have been associated with the triazines but resistance has now been identified with a wider range of herbicides. In 1982, Putwain (1982) reported the occurrence in the UK of eight populations of *Senecio vulgaris* and one population of *Poa annua* resistant to simazine, and one population of *P. annua* resistant to paraquat. Since 1982 the number of populations and species and the range of herbicides concerned has increased. For example, Moss and Cussans (1985) have identified inherited variation in resistance of *Alopecurus myosuroides* to chlortoluron. However, resistance to annual applications of non-persistent foliage-acting compounds (eg. phenoxy herbicides) has occurred only rarely (LeBaron & Gressel, 1982). Consequently it was considered unlikely that resistance to mecoprop would have arisen in *Galium aparine* or *Stellaria media* in the UK, despite the belief by farmers that poor control of these weeds was caused by resistance. Field experiments had confirmed that the performance of mecoprop in *G. aparine* was variable (Lovegrove *et al*. 1985) but it was not clear whether this was due to environmental, soil or biological factors. In consequence seeds were collected from ten sites including fields where performance had been good and poor, and from hedgerows where exposure to herbicides had been low. The performance of mecoprop on these ten *G. aparine* populations was assessed in two pot experiments, in order to assess whether there was variation in the intrinsic sensitivity of this weed. Similarly *S. media* from two fields where the performance of mecoprop had been inadequate was tested against a seed stock of 'normal' susceptibility in two further pot experiments. The performance of dichlorprop and MCPA was compared with mecoprop in the second of these.

MATERIALS AND METHODS

General

All experiments were carried out in a heated glasshouse and the seeds were sown in sandy loam soil in 9 cm pots. The seedlings were reduced to 10 plants/pot in all experiments except the Winchcombe population of *G. aparine*, tested in the second experiment, where inadequate germination resulted in only 8 plants/pot. A laboratory sprayer fitted with a single Spraying Systems 8002 TeeJet nozzle delivering 246 l/ha at 210 kPa was used for all herbicide applications. Details of the individual experiments are given in Table 1.

Following treatment, visual symptoms from the herbicides were recorded in all trials and fresh and dry weights were assessed 2-4 weeks after application. Herbicide effects were related to untreated control plants.

The Maximum Likelihood Programme (MLP) was used to fit Logistic Curves to the data, thus relating plant weight and log dose. From these curves the dose required to reduce plant weight by 50% was calculated (ED_{50}). Parallel curve analysis (Ross, 1978) was then used to assess the similarity of the curves of the different weed stocks.

TABLE 1

Experimental details

	G. aparine				*S. media*	
	Expt 1		Expt 2		Expt 1	Expt 2
	1st Appln	2nd Appln	1st Appln	2nd Appln		
Sowing date	11-20.1.84		18.9.84		18.9.84	30.1.85
Spraying date	22.2.84	5.3.84	18.10.84	19.10.84	19.10.84	6.3.85
Harvest date	16.3.84	20-22.3.84	8.11.84	28.11.84	8.11.84	26.3.85
Weed size at spraying						
Whorls	2-3	4-5	2-3	5	-	large
Nodes	-	-	-	-	3-4	plants
Branches	1 pr	2 prs	1 pr	3 prs	3-4	well branched
No replicates	7	6	5	5	6	3

Galium aparine experiments

Expt. 1.

Ten populations were studied: two samples (Chesterton, Kineton) were removed from contaminated grain, three samples were collected from hedgerow plants (Chesterton Hedge, Kineton Hedge, Yarnton), five were collected from plants taken from control plots of field experiments (Pitstone, Edlesborough, Winchcombe, Kingham, Walton). Mecoprop, potassium salt (570 g a.e./l; a.c.) was applied at two dates (Table 1) at five doses, 0.8-2.4 kg a.e./ha.

Expt. 2.

Five populations were selected for further studies in the second experiment (Walton, Edlesborough, Kineton Hedge, Kingham, Winchcombe). Mecoprop (potassium salt) was sprayed on two occasions (Table 1) at seven doses, 0.75-2.5 kg a.e./ha.

Stellaria media experiments

Expt. 1.

Two populations were studied in this experiment; 'Bath O', a reportedly resistant ecotype collected from a field near Bath where control from mecoprop had been unsatisfactory for two years, and 'WRO', the standard seed stock used in glasshouse experiments at the LARS Weed Research Division. Mecoprop (potassium salt) was applied at seven doses, 0.75-2.5 kg a.e./ha to the 'WRO' plants and at seven doses, 1.5-5.5 kg a.e./ha to the 'Bath O' plants.

Expt. 2.

A third population,'Bath N', from a field on an adjacent farm where mecoprop had failed to control S. media for several years, was included in this experiment which studied the activity of three related phenoxy herbicides. Mecoprop, potassium salt (570 g a.e./l; a.c.), was applied at nine doses, 0.3-2.7 kg a.e./ha to the 'WRO' plants and at ten doses, 1.8-7.2 kg a.e./ha to the plants from the two Bath populations. Eleven doses of dichlorprop, potassium salt (510 g a.e./l; a.c.), 0.05-2.52 kg a.e./ha were applied to the plants from the WRO population and eleven doses, 0.1-5.67 kg a.e./ha to those from the Bath populations. Plants from all three stocks received the same twelve doses of MCPA, potassium salt (320 g a.e./l; a.c.), 0.08-6.75 kg a.e./ha.

RESULTS

Although both fresh and dry weights were measured, only the fresh weight results are presented, as these showed most clearly the effects of the treatments.

Galium aparine experiments

Expt. 1.

The estimated doses that reduced G. aparine fresh weights by 50% (ED_{50}) were calculated for all seed stocks at both dates of mecoprop application. At the first date, the ED_{50} doses ranged from 0.46 kg a.e./ha on the most susceptible population (Winchcombe) to 1.2 kg a.e./ha on the least susceptible (Kineton Hedge). Higher doses 0.61-2.06 kg a.e./ha were required at the second application but the relative order of suceptibility, as shown by the ED_{50} values, was similar at both dates (Table 2). Plants from seed from Winchcombe, Walton and Chesterton Hedge appeared to be the most sensitive and those from Kineton Hedge and Kingham the least sensitive. However, the parallel curve analysis showed no significant displacement from a common curve and hence no difference between sources at both dates.

Expt. 2.

The results of this experiment were similar to those of the first one, G. aparine from Winchcombe and Walton being the most sensitive to both applications and Kingham tending to be the least sensitive. The response of the plants from Kineton Hedge differed at the two applications but their apparent greater susceptibility at the later application probably reflects the variability in the plants used for the later treatment. Again the standard errors of the log ED_{50} values were large and the parallel curve analysis indicated no significant differences between populations.

However, combined analysis of the ED_{50}s of the five sites from the two applications on both experiments indicated a significant difference between the most and least sensitive sites. Thus Winchcombe and Walton were more sensitive than Kingham and Kineton Hedge.

TABLE 2

Doses of mecoprop required to achieve 50% reduction in the fresh weight of G. aparine plants (kg a.e./ha)

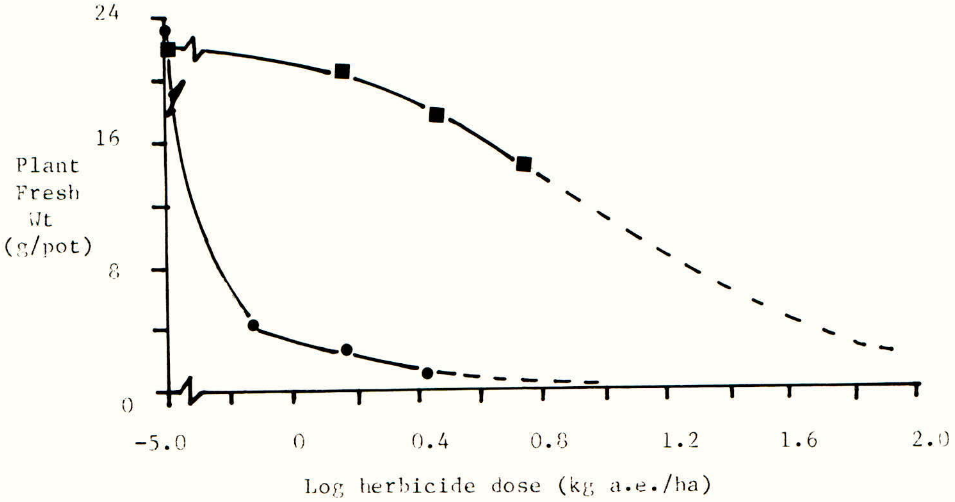
	Log ED_{50}	Log S.E.	Detransformed ED_{50} kg a.e./ha	Log ED_{50}	Log S.E.	Detransformed ED_{50} kg a.e./ha
Expt 1						
Seed Source	1st application (22.2.84)			2nd application (5.3.84)		
Winchcombe	-0.3362	0.0971	0.46	-0.2178	0.0837	0.61
Walton	-0.2458	0.1045	0.57	-0.0612	0.0510	0.87
Chesterton Hedge	-0.1400	0.0524	0.72	-0.0256	0.0404	0.94
Yarnton	-0.0723	0.0701	0.85	0.0771	0.0445	1.19
Pitstone	-0.0629	0.0463	0.86	0.1571	0.0579	1.43
Chesterton	-0.0512	0.0726	0.89	0.0724	0.1288	1.18
Kineton	-0.0473	0.0390	0.90	0.1725	0.0331	1.49
Kingham	0.0317	0.0487	1.08	0.1381	0.0640	1.37
Edlesborough	0.0333	0.0579	1.08	0.0389	0.1095	1.09
Kineton Hedge	0.0780	0.0518	1.20	0.3139	0.0340	2.06
Expt 2						
Seed Source	1st application (18.10.84)			2nd application (29.10.84)		
Winchcombe	-0.2783	0.0488	0.53	-0.4341	0.2353	0.37
Walton	-0.1737	0.0996	0.67	-0.2478	0.1390	0.57
Edlesborough	-0.1205	0.0834	0.76	-0.2250	0.0895	0.59
Kingham	0.0559	0.0435	1.14	-0.0769	0.0619	0.84
Kineton Hedge	0.0624	0.0934	1.15	-0.2818	0.1780	0.52

Stellaria media experiments

Expt. 1.

S. media plants from the 'Bath O' population were much more resistant to mecoprop than those from the 'WRO' population (Fig. 1). The ED_{50} value

(a) Experiment 1



(b) Experiment 2

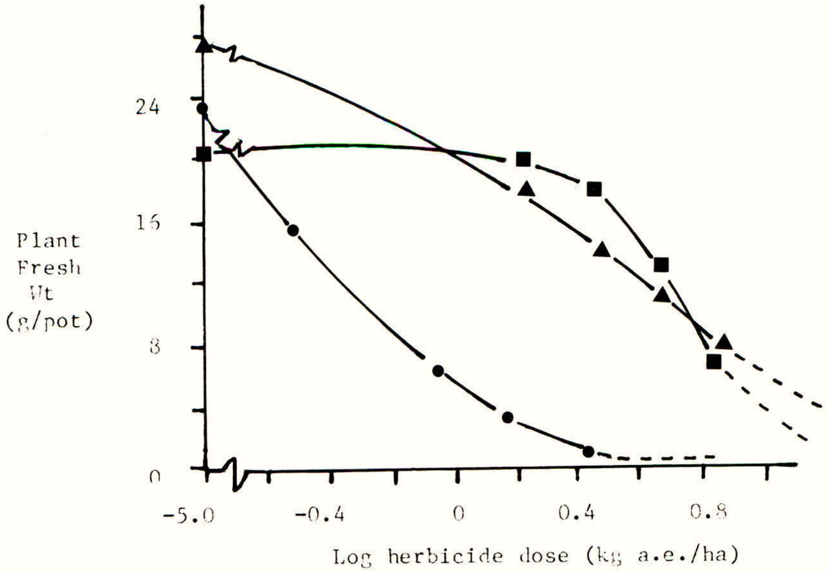
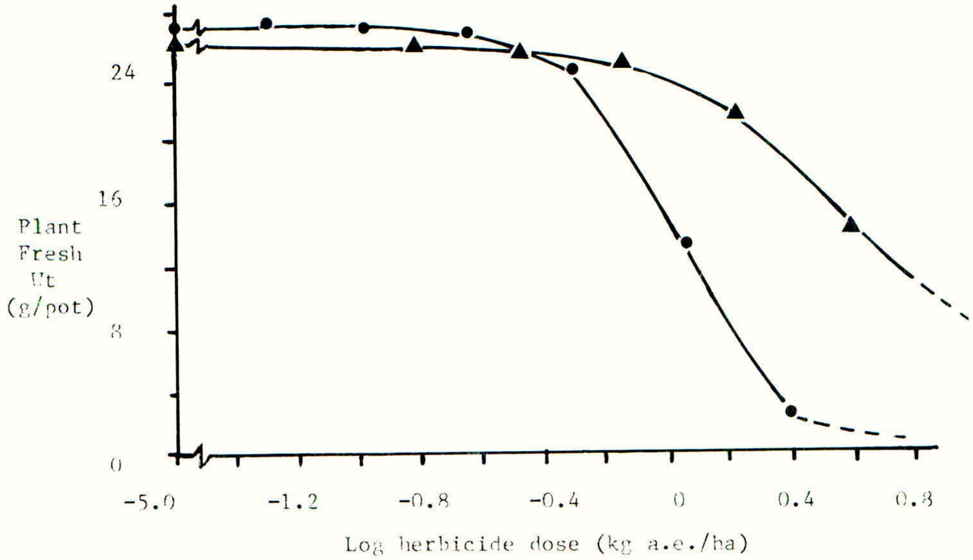


Fig. 1. Response of three populations of S.media to a range of doses of mecoprop. (a) Expt 1. (b) Expt 2. (●) WRO (■) Bath 'O' (▲) Bath 'N'

(a) Dichlorprop



(b) MCPA

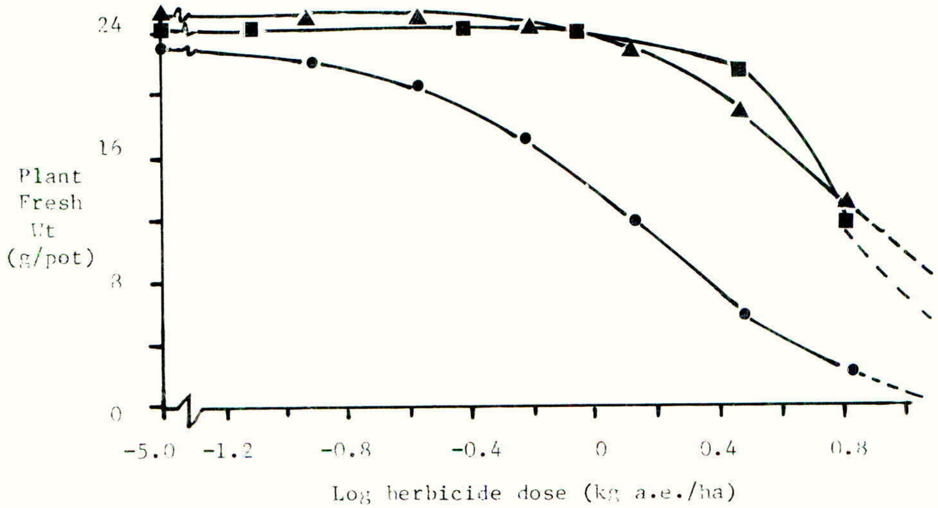


Fig 2. The response of three populations of *S.media* to (a) dichlorprop and (b) MCPA. (●) WRO, (■) Bath 'O', (▲) Bath 'N'.

for the 'Bath O' plants was 9.5 kg a.e./ha and that from the WRO plants was 0.2 kg a.e./ha. The parallel curve analysis showed that these two response curves were significantly different. Soon after application, the plants from the WRO population displayed typical epinastic twisting of leaves and stems whereas the 'Bath O' plants twisted very little but developed necrotic spots and patches on the leaves. At this time no necrosis was noted on the 'WRO' plants.

Expt. 2.

In this experiment MCPA, dichlorprop and mecoprop all caused severe epinastic twisting of the *S. media* plants from the WRO population. Only slight curling was noted from the higher doses applied to plants from the two Bath populations but all three herbicides caused the production of necrotic spots and patches on the leaves.

Doses of 5.6 and 6.4 kg a.e./ha of mecoprop were required to reduce the fresh weights of the *S. media* from the two Bath populations by 50% but only 0.45 kg a.e./ha was required for the 'WRO' plants (Fig. 1). Parallel curve analysis demonstrated that the responses of both the two Bath populations were significantly different from the WRO one. The ED_{50} value for the two Bath stocks treated with MCPA was 6.7 kg a.e./ha and that for WRO was 1.6 kg a.e./ha (Fig. 2). Again parallel curve analysis showed that the responses of the two Bath populations were the same and that these two were different from the WRO. The ED_{50} value for the dichlorprop sprayed on 'Bath O' plants was higher than the top dose so it was not possible to calculate a dose response curve. However, the 'Bath N' plants had an ED_{50} of 4.83 kg a.e./ha and the WRO 1.12 kg a.e./ha (Fig. 2). These were again statistically different.

DISCUSSION

The two *G. aparine* experiments showed no dramatic differences in response of the ten populations to mecoprop, although small differences appeared to be present, Winchcombe being significantly more sensitive than Kineton Hedge. Because of the level of variability in the data it was difficult to detect these differences except through combined analysis of the four applications. However, as these effects were small and the ED_{50}'s of the least susceptible only exceeded those of the most sensitive by a factor of 2-3, it is unlikely that these differences are the prime cause of unsatisfactory field performance, although they could contribute towards it. It is interesting to note that the population that tended to have the highest ED_{50} was Kineton Hedge, a hedgerow population exposed to little herbicide. This indicates that variation in the sensitivity of *G. aparine* populations to mecoprop is not related to their level of exposure to the herbicide and that the differences are not due to selection pressure resulting from the frequent use of mecoprop. The majority of the variation in field performance of mecoprop appears to be related to factors such as environmental conditions, soil type and crop competition rather than to variations in intrinsic susceptibility.

In complete contrast, the *S. media* from the two fields near Bath was considerably less sensitive to mecoprop than the standard 'WRO' plants. In the two experiments the ED_{50}'s of the Bath *S. media* were a 12-48 times greater than those for the WRO. In the second experiment this resistance to mecoprop was also reflected in greater, though less dramatic, resistance to dichlorprop and MCPA, where the ED_{50}'s of the Bath plants were four times those of the WRO ones. The absence of growth regulatory symptoms and the presence of necrotic spots and patches on the leaves of the Bath plants suggests that these herbicides were not acting within the plant in a normal way, and that the increased resistance could not be due solely to reduced retention or uptake. This conclusion is supported by further experiments (Liddle W. 1984, pers. comm.) which showed that differences in resistance were maintained even when the mecoprop was applied to the soil. The level of necrosis appeared from these experiments and those of Liddle to be related to temperature and light intensity, as more necrosis was recorded in spring and summer experiments than in autumn/winter ones. The reasons for the greater resistance of these two populations of chickweed needs further investigation. However, its practical importance is limited as a wide range of non-phenoxy herbicides are available to control these 'resistant' weeds.

The identification of resistance to mecoprop in the Bath S. media populations was unexpected as the non specific mode of action of the phenoxy herbicides does not encourage the development of resistance. In addition the 'Bath O' population comes from a predominantly grassland farm where mecoprop has been used only rarely. However, the 'Bath N' population was collected from a predominantly arable field where mecoprop has been used more often, although herbicide usage is not intensive. As the two farms are only a few miles apart it is a possibility that the original 'focus of resistance' has spread over a number of adjacent farms. A more detailed survey would be needed to clarify the distribution of resistant types.

In conclusion, the four experiments have demonstrated that resistance to mecoprop can occur in broad-leaved weeds but they have not shown that repeated use of this herbicide is likely to be the cause. Poor field performance from mecoprop, particularly on cleavers, is more likely to have been the result of factors unrelated to the intrinsic susceptibility of the weed.

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THE INFLUENCE OF MORPHOLOGY OF GALIUM APARINE ON THE UPTAKE AND MOVEMENT OF CLOPYRALID AND FLUROXYPYR

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ABSTRACT

The uptake and translocation of ^{14}C-fluroxypyr and ^{14}C-clopyralid (both discoveries of the Dow Chemical Company) from 3 regions of application to Galium aparine was studied. Fluroxypyr, which killed G.aparine at the 2-3 whorl stage entered the plant rapidly in ester form with up to 77% uptake after 7 days. Uptake was most rapid from the leaf whorls, particularly the youngest whorl which retained most herbicide (40% of spray). Herbicide applied to the 1st and 2nd whorls moved to the main shoot apex and developing leaves whilst that applied to the cotyledons moved largely into the lateral shoots developing from the cotyledon node. Fluroxypyr was recovered from the apex in the acid form and as undefined polar conjugates. Field rate clopyralid was less effective on G.aparine than fluroxypyr. Clopyralid uptake was slower, reaching up to 13% after 7 days and there were no significant differences in uptake between sites of herbicide application. 90% of the penetrated clopyralid was translocated with a similar distribution pattern to fluroxypyr. 85% of clopyralid recovered from the plant apex was in the form of unchanged acid or acid-conjugates. In a bioasssay system fluroxypyr was found to be more active on Galium aparine apical tissue than clopyralid.

INTRODUCTION

Galium aparine L. (Cleavers) has increased in agronomic importance since the widespread use of substituted ureas to control Alopecurus myosuroides (black-grass) in cereals (Makepeace 1982). In a recent survey it was found to be the second most frequent broad-leaved weed present in cereal crops, occurring in 12% of the winter wheat fields surveyed (Chancellor & Froud-Williams 1984). The competetive ability of this species is due to the presence of deflexed prickly bristles on the stem which enable it to cling to and climb up and over other plants (Hanf 1983). An infestation of G.aparine can cause substantial reduction in yield, interfere with harvesting, and reduce yield quality through seed contamination (Froud-Williams 1985).

G.aparine has proved a difficult weed to control in winter cereals (Bradford & Smith 1982), with the most acceptable results achieved with foliar applications of either mecoprop alone, or mecoprop mixed with the hydroxybenzonitriles. The recently introduced pyridine herbicide, fluroxypyr controls G.aparine at 150-200 g ai.ha^{-1}, and is more effective than the structurally similar clopyralid. In this paper, the activity of these two herbicides (both discoveries of the Dow Chemical Company) will be compared and related to the morphology of G.aparine. This will involve a study of the uptake and movement of clopyralid and fluroxypyr from the major sites of spray interception, and an investigation of the metabolism and physiological activity of the herbicides in G.aparine.

MATERIALS AND METHODS

Treatment of plants

Galium aparine seeds were sown at a depth of 5 mm in 90 mm pots containing J. Arthur Bowers potting compost. The pots were maintained under glasshouse conditions and plants were thinned to 2 per pot at the young seedling stage. When the cotyledon leaves and the 1st leaf whorl had emerged, the pots were transferred to an environmental chamber (Fisons Model 600G3, type TTL) 14 h day 20°C and 100 $\mu E.m^{-2}.s^{-1}$ (PAR), 10 h night 14°C. In all experiments plants were treated when the 2nd whorl was fully developed and the 3rd whorl was visible. The presence of 2 lateral shoots emerging from the cotyledon node (node 1) was characteristic. In all spray experiments, clopyralid as Lontrel* and fluroxypyr as Starane 2* were applied at a dose rate equivalent to 150 g $ai.ha^{-1}$ and 200 $l.ha^{-1}$ using a hydraulic laboratory pot sprayer (Mardrive Marine Engineering Co Ltd) fitted with an 80° T-jet nozzle. Spray retention was determined using an aqueous solution of tartrazine (Pallett & Caseley 1980).

Uptake and translocation of ^{14}C-clopyralid and ^{14}C-fluroxypyr

^{14}C-pyridine-ring labelled clopyralid and fluroxypyr 1 methylheptyl ester (MHE) were used to determine uptake and movement from the cotyledon, and 1st and 2nd whorls of G.aparine. Prior to treatment with radiolabelled herbicide, selected regions of the plant were covered with polythene and the plants were sprayed with field rate herbicide. After drying, the polythene was removed, and 0.2 µl droplets of ^{14}C-clopyralid and ^{14}C-fluroxypyr (diluted with field rate herbicide) were applied to the untreated regions. Approximately 20,000 dpm were applied to each plant as either five 0.2 µl droplets to one of the cotyledons, or one 0.2 µl droplet to each leaf of the 1st or 2nd whorl. After 1, 3, and 7 days residual (unpenetrated) herbicide was washed from the leaf surface by successive washes with blank formulation and chloroform, and counted for radioactivity as previously reported (Sanders & Pallett 1985). Each plant was divided into sections as illustrated in Fig. 2 (with the stem below each section included with that section) and radioactive content determined as previously described (Sanders & Pallett 1985).

Metabolism

Fifteen to eighteen 0.2 µl droplets of ^{14}C-clopyralid and ^{14}C-fluroxypyr MHE (≡ 200,000 dpm) were applied to the cotyledons and 1st whorl of G.aparine. After 7 days, the apex and emerging whorls of 6 plants were finely homogenised in a small volume of acetone (0.5-1 ml) in a prechilled pestle and mortar. Each homogenate was centrifuged at maximum speed for one min in a microfuge (MSE MicroCentaur) and the resulting supernatents were concentrated in a N_2 stream to 100 µl. Thirty to forty µl of each supernatent were spotted onto a precoated plastic TLC plate (Merck Kieselgel 60F254) and the plates were developed in either 80 chloroform : 20 methanol : 1 glacial acetic acid (clopyralid extracts) or 50 hexane : 50 ethyl acetate : 3 glacial acetic acid (fluroxypyr extracts). After development a 15 mm wide strip, within which the extract had migrated, was excised from the plate and sectioned into 5.0 mm portions. Each portion was placed in 5 ml of Optiphase Safe scintillant (Fisons) and counted for radioactivity. In the solvent systems used fluroxypyr MHE and fluroxypyr (acid) had Rf values of 0.69 and 0.30 respectively, and clopyralid had an Rf value of 0.2.

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*Trademark of the Dow Chemical Company

Bioassay

0, 10^{-6}, 10^{-5}, 10^{-4} and 10^{-3} M solutions of clopyralid (acid) and fluroxypyr (acid) were prepared in 1/5th strength Nitsch's medium and adjusted to pH 6 with NaOH. 9 ml of each solution was placed in a 5 cm petri dish and covered with self-sealing film. 8 replicate 20 mm portions of *G.aparine* shoot tip (with leaves removed) were inserted into each solution to a depth of 5 mm. Each shoot tip was measured for extension growth following a 48 h incubation in a controlled environment chamber.

RESULTS

Foliar applications of fluroxypyr and clopyralid induced differing symptoms in *G.aparine*. Within 1 day of fluroxypyr treatment, there were nastic symptoms in the stem and lateral shoots and within 7 days, the stem was swollen and necrotic, the cotyledons and 1st whorl exhibited some chlorosis, and there was no further growth of the apex and lateral shoots. Conversely, following an initial curvature of the developing whorls of the main shoot and laterals, clopyralid treated *G.aparine* exhibited extensive regrowth of lateral shoots with some continued main shoot growth.

The influence of morphology of *G.aparine* on the interception of foliar sprays was investigated using the water soluble dye, tartrazine. *G.aparine* with 2-3 whorls retained 25 µl of dye per plant (Table 1) of which 38% was retained by the 2nd whorl, 27% by the 1st whorl and 13% by the cotyledons. Contact angles were comparable for the two formulated herbicides (clopyralid 50.4 ± 2.33, fluroxypyr 47.8 ± 0.94) and were also similar on the cotyledons and whorls (data not presented).

TABLE 1

Tartrazine dye retention by *G.aparine*

	Cotyledons	Whorl (1)	Whorl (2)	Remainder of plant	Total
µl Retained	3.38 ±0.25	6.79 ±0.95	9.85 ±0.47	5.41 ±0.05	25.43 ±1.61

Data is a mean of 6 replicates and includes standard errors.

Differences were observed in the rate of uptake of the two herbicides (Fig. 1). ^{14}C-fluroxypyr uptake reached a maximum of 78%, 7 days after treatment and was 6-10 times greater than ^{14}C-clopyralid uptake. In addition, ^{14}C-fluroxypyr uptake by the 1st and 2nd whorls was approximately twice as much as by the cotyledons. In contrast however there was a similar rate of ^{14}C-clopyralid uptake at each site of application. Differences were also observed in the proportion of ^{14}C-activity detected in the cuticle of *G.aparine*. After one day, 57% of the applied ^{14}C-fluroxypyr was present in the cuticle of the cotyledons compared to 1.3% of the ^{14}C-clopyralid, and at all sites of application there was more ^{14}C-fluroxypyr than ^{14}C-clopyralid detected in the chloroform extract (data not presented).

The enhanced rate of ^{14}C-fluroxypyr uptake was confirmed when the ^{14}C-herbicide treated plants were sectioned and counted for radioactivity (Fig. 2). One day after cotyledon treatment 2.08% of the applied ^{14}C-clopyralid and 4.15% of the applied ^{14}C-fluroxypyr were detected in the

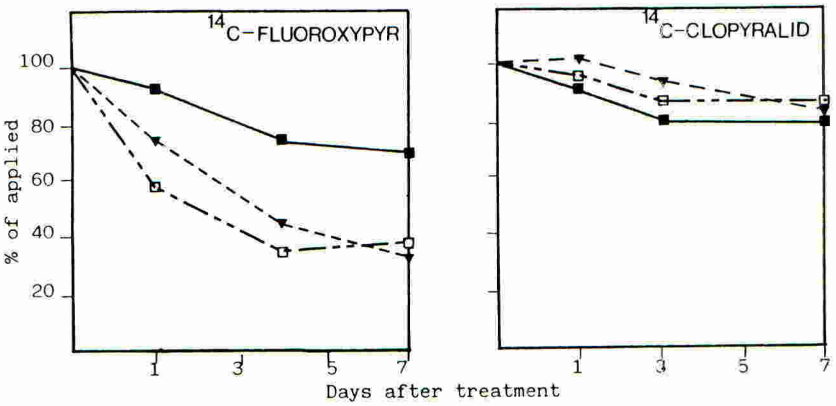

Fig. 1. The uptake of ^{14}C-fluroxypyr and ^{14}C-clopyralid by the cotyledons (—■—), 1st whorl (--▼--) and 2nd whorl (·-□--) of G.aparine. Data is expressed as the percentage of applied ^{14}C-herbicide recovered from the leaf surface and cuticle of each tissue.

cotyledon leaves. An additional 2.2% of ^{14}C-clopyralid and 3.8% of ^{14}C-fluroxypyr was translocated out of the cotyledon, mainly to the newly emerging laterals and also to the developing whorls. After 7 days, a further 0.56% of ^{14}C-clopyralid and 11.50% of ^{14}C-fluroxypyr were detected in the treated cotyledons. The laterals were the primary sinks for both herbicides, although significant amounts of ^{14}C-fluroxypyr were also translocated to other regions of the plant (Fig. 2). Following application to the first whorl, the proportion of ^{14}C-clopyralid and ^{14}C-fluroxypyr recovered from the whorl leaflets was 0.45% and 6.13% respectively after one day, and 0.60% and 18.16% respectively after 7 days. At each harvest, a higher proportion of the translocated ^{14}C-herbicides were detected in the youngest whorl and apex, than in the lateral shoots. Fluroxypyr was also extensively translocated to other regions of the plant and after 7 days 4.03% was detected in the 2nd whorl and 5.69% was detected in the cotyledons. Greatest ^{14}C-fluroxypyr uptake and movement occurred following application to the 2nd whorl. After 1 day, 17.29% was detected in this whorl and 19.7% had been translocated, and after a further 6 days 15.35% was detected in the treated whorl and 62.1% of the applied ^{14}C-fluroxypyr was translocated to other regions of the plant. In comparison, 0.7% of ^{14}C-clopyralid was present in the treated leaflets and 2.6% was translocated at the 1 day harvest, and by 7 days 0.59% was detected in whorl 2, and 8.02% was translocated. The main shoot apex was the primary sink for both herbicides after 1 day and ^{14}C-fluroxypyr after 7 days, whereas the apex and laterals were of similar importance as sinks for ^{14}C-clopyralid 7 days after treatment.

The apical tissue of ^{14}C-clopyralid and ^{14}C-fluroxypyr treated plants was assayed to determine the chemical nature of the translocated ^{14}C-label. 60% of the radioactivity extracted from ^{14}C-clopyralid treated plants was associated with a compound of Rf value 0.20 identified as clopyralid (Fig. 3), and approximately 20% was associated with compounds less mobile in this solvent system, thought to be polar conjugates. A third unidentified less polar metabolite of Rf value 0.52 accounted for 10% of the radioactivity extracted from clopyralid treated plants. ^{14}C-fluroxypyr MHE (Rf 0.69) was applied to the leaves of G.aparine but was not detected in the apical region extract, however a compound of Rf value 0.30 identified as fluroxypyr

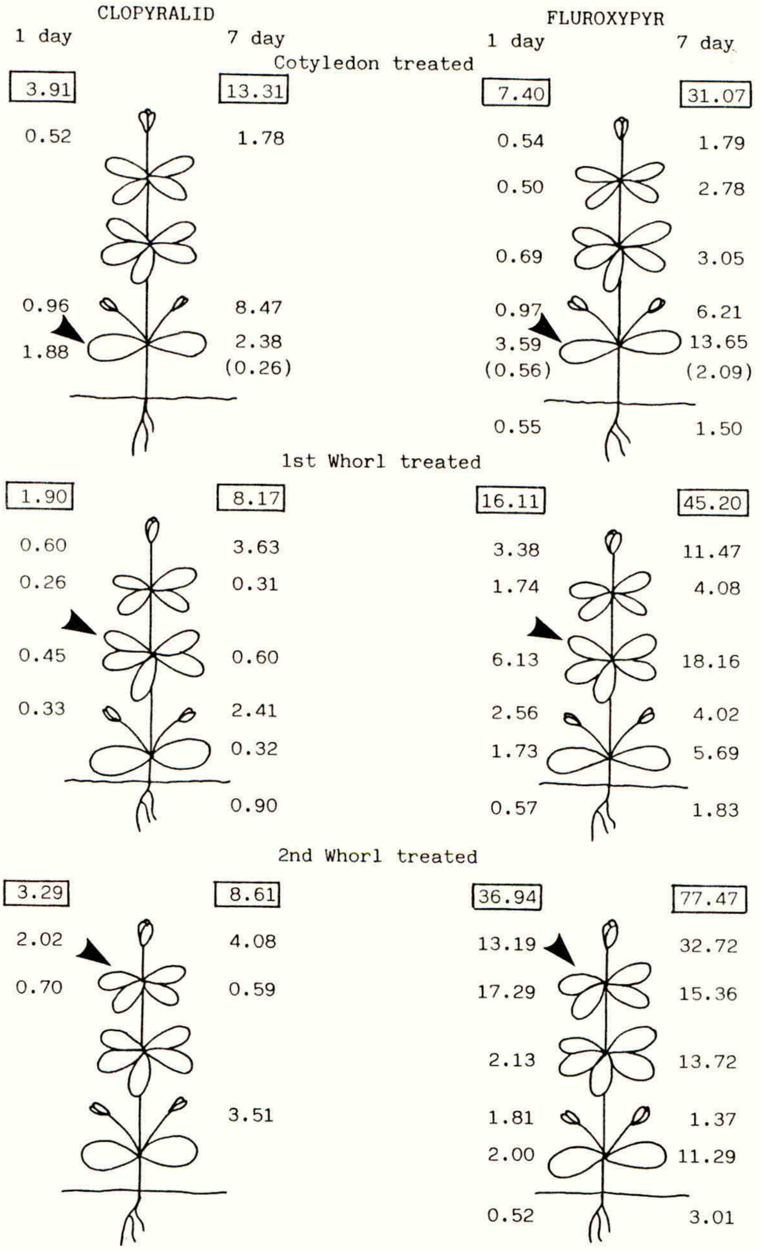

Fig. 2. The distribution of ^{14}C-activity following ^{14}C-clopyralid and ^{14}C-fluroxypyr treatment of G.aparine. Figures represent % of applied activity recovered from the plant parts, where > 0.20%. Data is a mean of 6 replicates and standard errors were < 10% of mean values. The figures in boxes represent total ^{14}C-activity recovered from the plant expressed as % of applied, and the figures in brackets represent the % detected in the untreated cotyledon following application to the opposite cotyledon.

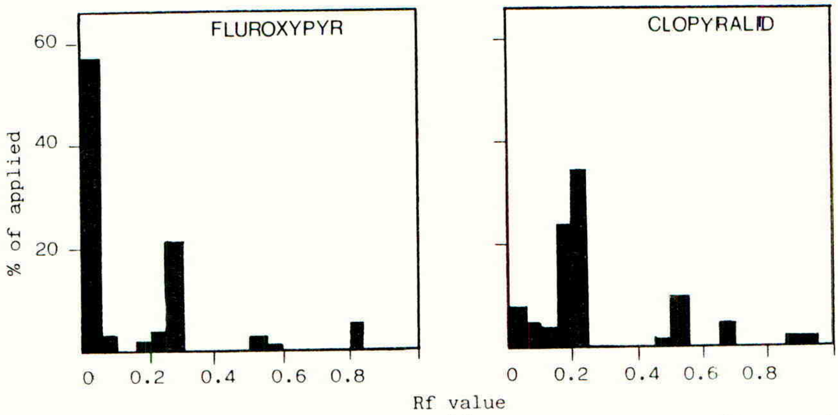

Fig. 3. T.L.C. of ^{14}C-fluroxypyr and ^{14}C-clopyralid metabolites extracted from the apex and emerging whorls of G.aparine.

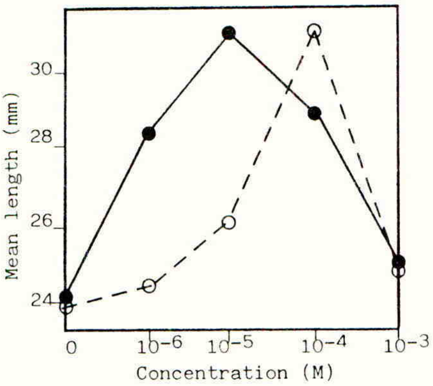

Fig. 4. Extension of G.aparine shoot explants 48 hours after incubation in fluroxypyr (—●—) and clopyralid (-○-).

(acid) was present, and accounted for 21% of the radioactivity. The highest level of radioactivity was detected at the origin representing polar conjugates of fluroxypyr (acid) which are immobile in the solvent system used.

Extensive elongation and nastic movement of apical tissue are typical symptoms of all auxin-type compounds, and an explant system was developed to compare the activity of the two herbicides without the influence of uptake, movement and metabolism. In this system clopyralid and fluroxypyr (acid) promote elongation of G.aparine shoot explants at concentrations ranging from 10^{-6} to 10^{-4} M (Fig. 4). Maximum elongation occurred at 10^{-5} M fluroxypyr and 10^{-4} M clopyralid, and no significant elongation occurred at 10^{-3} M.

DISCUSSION

G.aparine was used for experimentation when 2-3 whorls had developed on the main stem and lateral shoots were emerging from the first node. Seven days after treatment, untreated control plants exhibited extensive lateral growth from the 1st, 2nd and 3rd nodes, and laterals were also emerging from nodes 4 and 5. Effective control of G.aparine requires the herbicide to be translocated to the apex and laterals and interfere with their development. In this study, fluroxypyr completely inhibited main shoot and lateral growth, whereas clopyralid reduced the growth of the main shoot only, and only partially inhibited the emergence and development of new lateral shoots. The morphological and physiological basis for this difference was investigated.

Dye retention data (Table 1) indicates greatest retention of herbicides by the 2nd whorl and progressively less by the 1st whorl and the cotyledons. Differences were observed in the rate of fluroxypyr uptake by each of these sites (Fig. 1), with the greatest uptake occurring in the tissues which also retained the most herbicide. Enhanced uptake by younger leaves has been reported for other herbicides, and is commonly related to changes in cuticle thickness and chemical composition as the leaves mature (Sargent & Blackman 1972, Norris 1974). In contrast, clopyralid uptake was similar at each site and considerably lower than fluroxypyr uptake. This is likely to reflect differences in the formulation and chemical nature of the herbicide molecule since fluroxypyr is applied as the 1-methylheptyl ester, and clopyralid is applied as the monoethanolamine salt. It is well established that the less polar and more lipophilic ester forms of other auxin-type herbicides are absorbed more rapidly than the hydrophilic amine and acid forms (Richardson 1977). The lipophilic nature of fluroxypyr MHE is confirmed by the high proportion of radiolabelled herbicide detected in the cuticle extract 1 day after treatment.

Extraction of ^{14}C-labelled compounds from the apical region of treated plants has revealed that fluroxypyr MHE is hydrolysed within the leaves into fluroxypyr acid and it is this compound or polar conjugates which are translocated (Fig. 3). Clopyralid was found to be largely translocated as the unmetabolized acid form, as recently shown in Cirsium arvense (Turnbull & Stephenson 1985). This may partially explain why proportionately more of the penetrated clopyralid is translocated out of the treated leaf (Fig. 2), since an initial conversion into a phloem-mobile form is unnecessary.

The site of spray interception by G.aparine was found to greatly influence the direction of translocation of clopyralid and fluroxypyr. Herbicide penetrating the cotyledons was primarily translocated to the laterals developing adjacent to the cotyledons, whereas herbicide absorbed by the 2nd whorl was mainly translocated to the shoot apex (Fig. 2). Interestingly absorption by the first whorl led to translocation to the apex and laterals, with the shoot apex the more important sink. These differences in the distribution of translocated clopyralid and fluroxypyr most probably reflect the source:sink relationships of assimilate translocation in G.aparine. The cotyledons and to a lesser extent the first whorl may export assimilates which are used for lateral shoot growth, whereas assimilates produced in the upper whorls may be utilized in the development of leaf primordia at the main shoot apex. In a similar study, clopyralid absorbed by the upper leaves of Cirsium arvense was translocated to the apex, and herbicide absorbed by the lower leaves was translocated to the root of this perennial weed (O'Sullivan & Kossatz 1984). The enhanced activity of fluroxypyr against G.aparine may also be related to it's extensive translocation throughout the plant, as well as to major sinks.

Both clopyralid and fluroxypyr are therefore translocated to the growth points of G.aparine, but it is only fluroxypyr which inhibits further development of laterals and new leaf primordia. This may simply reflect the higher levels of fluroxypyr in these sensitive tissues (Fig. 1) causing a greater hormonal imbalance, or additionally may be indicative of an inherent sensitivity of G.aparine to fluroxypyr. The exact mechanism of action of auxin-type herbicides has not been fully elucidated but it is well established that these herbicides rapidly promote proton release from the plasmalemma resulting in cell elongation. Additionally, other auxin sensitive processes are affected which leads to aberrant nucleic acid metabolism and ultimately to plant death (Pillmoor and Gaunt 1980). Fluroxypyr (acid) is ten times more active towards elongation than clopyralid (Fig. 3) and probably to the other auxin sensitive processes contributing to herbicide action. Thus the enhanced uptake and translocation of fluroxypyr, and increased sensitivity of G.aparine to fluroxypyr may explain why this herbicide is more effective than clopyralid in controlling G.aparine.

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