

# **SESSION 9A**

## **W WEED COMPETITION AND THRESHOLDS – FUNDAMENTAL ASPECTS OF COMPETITION AND POPULATION DYNAMICS**

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SESSION  
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INVITED PAPERS      9A-1 to 9A-2

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## THE POPULATION ECOLOGY OF WEEDS - IMPLICATIONS FOR INTEGRATED WEED MANAGEMENT, FORECASTING AND CONSERVATION

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## ABSTRACT

The role of population ecology in understanding the dynamics of weed populations is assessed in relation to strategic forecasting and conservation. Approaches to modelling population trajectories under differing weed management practices are briefly discussed and a methodology for predicting long term dynamics illustrated. Future strategic research needs are commented upon in relation to the application of such studies to agriculture.

## INTRODUCTION

Population ecology is that branch of ecology ( Greek : *oikos*, home / house; *logos* , study) that seeks to expose the factors that regulate species abundance in 'households' through time and space (Begon and Mortimer 1985). In the context of weeds this 'household' is the agroecosystem and it is one which has come under increasingly close scrutiny during this decade. Calls for the rational management of weeds (both economic and ecological) have arisen from the alternate pressures for the need to optimise inputs in agricultural systems (Robinson 1978) and concern for the protection of the environment. This paper briefly reviews the the potential benefits that studies of the population ecology of weeds may bring to agriculture focussing on homogeneous cropping systems (Snaydon 1980).

## THE PRAGMATIC CONSIDERATIONS OF WEED MANAGEMENT.

Based on a range of sources (eg Attwood 1980; Elliott 1982) the criteria of decision making in weed control may be summarised under four general questions :

1. In a given cropping and weed management regime, how likely is it that invasion by weed species will occur and conversely can species of conservation value be retained within the agro-ecosystem ?
2. Given the presence of an infestation, how fast will the size of the weed infestation change (increase or decline) under different management strategies and how much damage (in all senses) will the crop suffer ?
3. How much of a proposed control measure is required to
  - a) contain the weed infestation at its current size, or
  - b) force the population into a decline so as to cause ultimate eradication ?

4. What are the comparative costs of different weed management strategies and what are the risks associated with alterations in control practices?

These questions are couched in general terms and belie the explicit issues that may be raised by consultants and growers. Yet questions such as ' Will minimum tillage favour weed species "A" over "B" ', ' Will chemical "Y" eradicate species "C" quicker than chemical "Z" ' or ' Is it economic to spray every year against species "D" ' are easily seen as specifics within the general scheme.

## THE ECOLOGICAL BACKGROUND

Agroecosystems as 'households' for weeds comprise habitat mosaics on a large spatial scale with components often displaying fidelity both in land use and species composition. Such mosaics are a direct consequence of agricultural management practices, each component offering radically different probabilities of mortality and fecundity to a species. Whilst hedgerow and crop flora attest in a historical fashion to this, critical observations and experimental evidence suggest that management practices are very powerful forces of interspecific (eg Haas and Streibig 1982; Froud-Williams and Chancellor 1984) and intergenotypic (eg Putwain *et al.* 1982 ) selection. Past management practice may well have reduced the weed community within the crop to a depauperate collection of 'difficult' species and designated surrounding land to the role of 'reservoir' for natural vegetation. Moreover the spatial distribution of weeds within the crop may be patchy. Two particular requirements of population ecology then, are to explain 'how' such forces operate and 'why' vegetation change results, being specifically concerned with changes in species abundance over time and in spatial location. The forthcoming answers are potentially of equal value when applied both to the conservation of natural flora as to the optimisation of crop yield.

A baseline for predicting whether a plant population will increase or decline in the long term requires measurement of its finite rate of increase or per capita multiplication rate,  $\lambda$ . (For  $\lambda > 1$  the weed population will increase in size, whilst in a static population  $\lambda = 1$ . Conversely  $\lambda < 1$  indicates a population in decline. In annual plants with discrete generations and no seed bank, measurement of  $\lambda$  is straightforward. It involves census of the population  $N$  at intervals ( $t$  and  $t+1$ ) which encompass a complete generation;  $\lambda$  is then the proportionate change,  $N_{t+1} / N_t$ . For species with overlapping generations and/or seed banks the procedures are more involved). Any measurement of  $\lambda$  is however a reflection of the the habitat conditions experienced by the population during a generation and of the distribution of resources for growth to individual members of the population. It is now well recognised in theory at least that in a population 'left to its own devices',  $\lambda$  diminishes with increasing population size with the result that a stable equilibrium population size may be reached. The expectation rests on the assumption that all other features of the habitat remain constant and intrinsic biotic regulation within the weed population restricts  $\lambda$ .

Where a species maintains stability in abundance within a habitat ( $\lambda=1$ ), Watt (1947) recognised that there was a persistent spatial shuffle of individual plants in the community on a local scale. This view has led to the suggestion, for a species to persist within a habitat there may be a critical minimum habitat size in which the effects of emigration and death are balanced by immigration and birth. The divisive nature of agricultural management practices reinforces the view that habitat islands exist within agro-ecosystems and suggest that species gain and loss may obey the principles of island biogeography (MacArthur 1972).

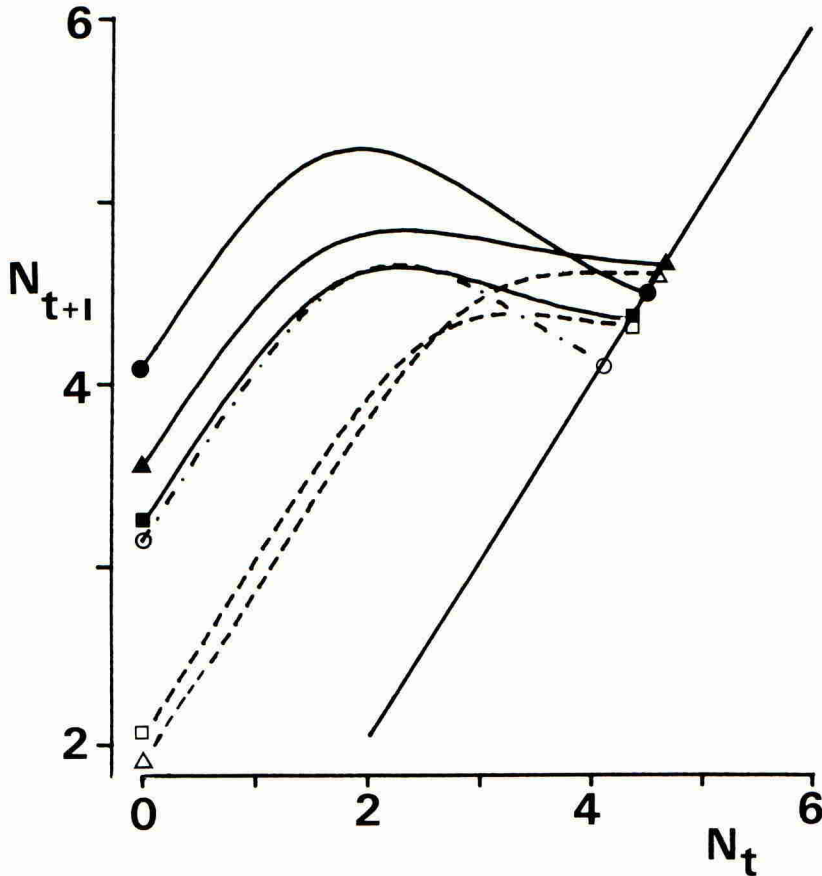


Fig. 1. Changes in population size over generations ( $N_t$  to  $N_{t+1}$ ) in three weed species. Triangles, *Agrostemma githago* in a pot experiment, closed - in monoculture, open - in wheat (data from Watkinson 1981); squares, *Bromus sterilis* in a field trial, - closed in monoculture, open - in winter wheat (from Firbank et al. 1984); circles *Senecio vulgaris* in a pot experiment, closed - biotype sensitive to simazine, open - biotype resistant to simazine (from Watson 1987). Units are 'seed'  $m^{-2}$  expressed on  $\log_{10}$  scales, curves being derived from fitted models. Solid diagonal line is of unit slope. In all cases no loss of seed from dispersal through to germination is assumed.

## APPLICATION OF POPULATION DYNAMICS

What then is the practical relevance of these concepts? Four major points of pragmatic worth immediately arise out of studies of population dynamics.

Calculating rates of increase of weed infestations

Knowing the growth rate of a weed population enables comparative assessment amongst weed species and qualitative prediction of the size of future populations. Fig. 1 gives some examples of the changes in population size that have been measured for three species in the absence of deliberate weed control. They are calculated on the assumption that the habitat conditions other than changes in weed density remain the same. The curves illustrate three important points. First that density dependent regulation can act strongly to regulate the size of populations. Cobwebbing  $N_t$  to  $N_{t+1}$  successively up the curve leads to the equilibrium point in a very few generations. Second that equilibrium population sizes may be lower than intermediate ones and third that the presence of an associated species (here a crop) may alter the trajectory of population increase.

Similar maps of generation to generation change are given in Figs 2 and 3 for *Avena fatua* and *Alopecurus myosuroides* in field plots of winter wheat experiencing post emergence herbicides. For *A. fatua* (Fig. 2) finite rates of increase greater than one (ie population increase) were recorded across all infestation densities and the herbicide appeared to act in a density independent way. In *A. myosuroides* (Fig .3) different trajectories were observed according to rate of herbicide application. With application of half the recommended rate of chlortoluron, at low infestation densities finite rates of increase were observed to be less than unity (population decrease) at low infestation densities and greater than unity in higher infestations. At recommended rate, however the relationship between successive population sizes was far less clear. Field observations taken during the experiment showed this result to be due to a very few plants surviving herbicide application to set seed (P.F.Ulf-Hansen, pers comm.).

Comparing management practices - sensitivity analysis

The trajectory of the curve governing changes in per capita rates of increase will be governed by the interaction of density dependent and density independent regulatory agencies that are the net result of all crop husbandry and weed management practices used. Families of such curves under a range of management practices provide the opportunity for comparative evaluations of alternative management practices *in toto*. Their actual construction requires 1) measurement under field conditions of the rates of increase of weed population growth over a wide range of infestation densities; 2) the statistical fitting of an appropriate model to the relationship and; 3) verification of the model. Once achieved, stability analysis can be conducted to examine the sensitivity of the population to changes in parameters that may arise through altering efficiency of control. The difference equation,

$$N_{t+1} = \lambda \cdot N_t (1 + a \cdot N_t)^{-b} \quad (1)$$

provides a satisfactory fit to the data in Fig.2 .  $\lambda$  is the finite rate of increase of an isolated plant and  $a$  and  $b$  are parameters which describe the species response to increasing density. Equation 1 may be extended to include the influence of control practices. One such way is

$$N_{t+1} = \lambda \cdot N_t (1 + a \cdot N_t)^{-b} - \Lambda N_t \quad (2)$$

where  $\Lambda = \rho \lambda$ . The model assumes that control is exerted as a proportion,  $\rho$ , of  $\lambda$  and is independent of weed density. Fig. 4 illustrates the stability domains of the

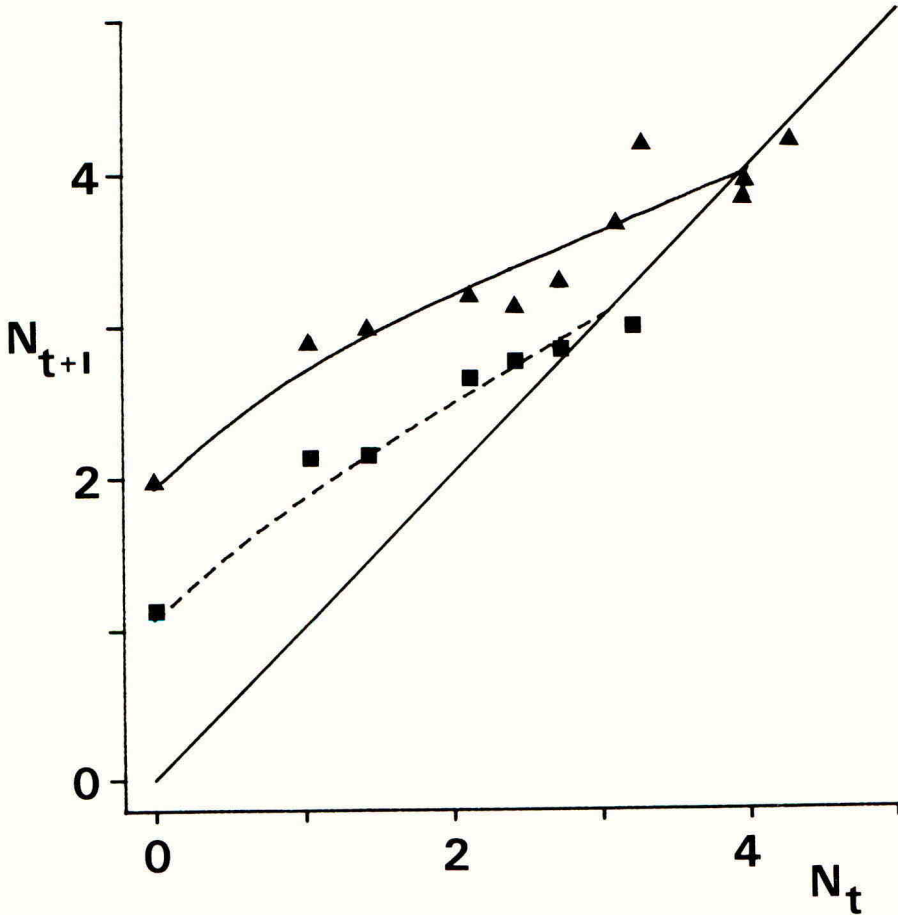


Fig. 2. Changes in population size in *Avena fatua* growing in winter wheat (data from Manlove, 1985). Squares, populations sprayed with 1 - flamprop - isopropyl at 3 l / ha in 450 l / ha water applied post emergence in late season; triangles, unsprayed populations. Fitted lines are  $N_{t+1} = \lambda \cdot N_t \cdot (1 + a \cdot N_t)^{-b}$  after Hassell (1975) and census units are seeds  $m^{-2}$  after crop harvest, expressed on  $\log_{10}$  scales.  $R^2$  is the coefficient of determination.

	$\lambda$	$a$	$b$	$R^2$
Control	96.7	0.194	0.593	0.98
Sprayed	13.2	0.228	0.429	0.97

model and allows prediction of the long term outcome under various efficiencies of control. One simple application is as follows. Given description of the population dynamics of a weed experiencing intrinsic regulation in the absence of a proposed control we may predict for a particular intensity of control whether a population will be unable to achieve a steady state equilibrium (and in theory decline to extinction) but if so, what it will be in the long term. A test of prediction may be conducted with the data for *A. fatua* (Fig .2). Given estimates of  $\underline{a}$  and  $\underline{b}$  from unsprayed plots and

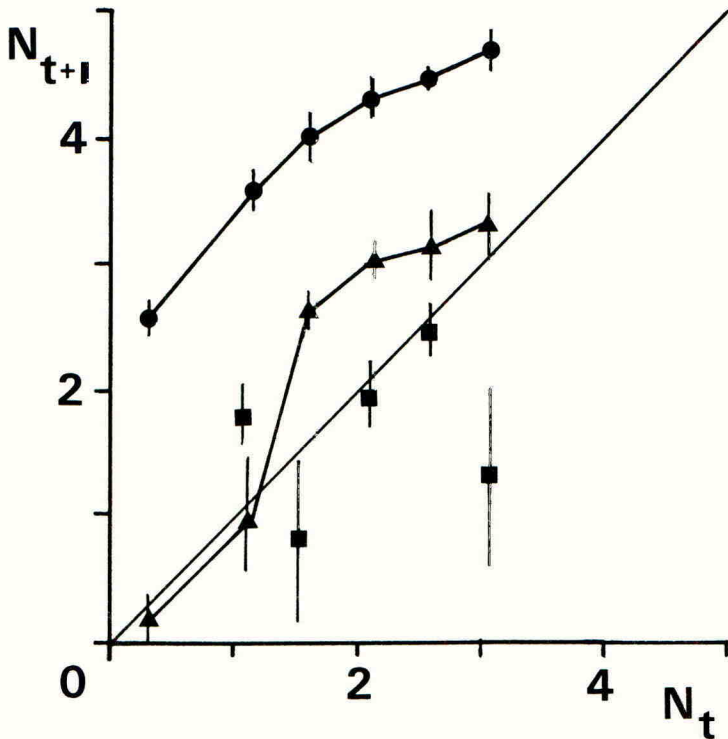


Fig.3. Changes in population size (seeds  $m^{-2}$  on  $\log_{10}$  scales) in *Alopecurus myosuroides* growing in winter wheat (data of P.F.Ulf-Hansen). Circles unsprayed control; triangles half rate and squares full rate (2.75 l a.i. / ha) chlortoluron. applied post emergence. Means are  $\pm 1$  s.e. The population follows the trajectory  $N_{t+1} = 272 N_t (1 + 0.008N_t)^{-0.81}$  when unsprayed ; and  $N_{t+1} = 2029.9 N_t^2(15190.2 + N_t^2)$  under half rate chlortoluron.

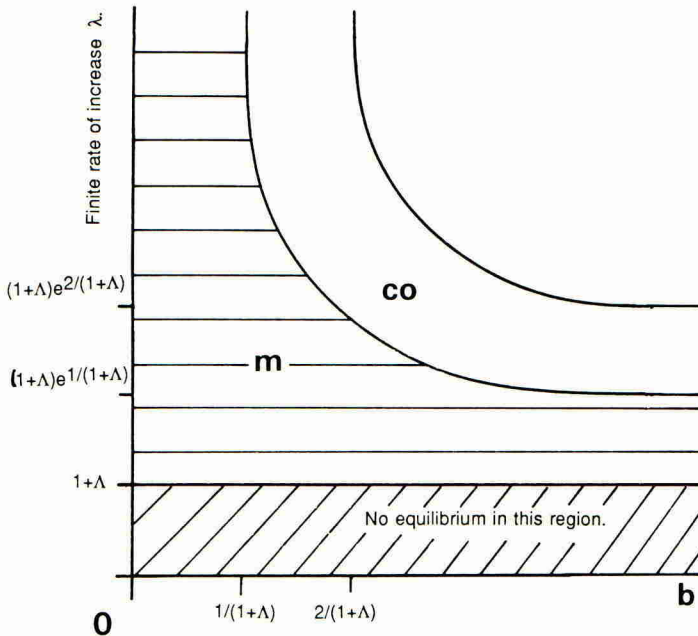


Fig. 4. The stability regions for a population governed by

$$N_{t+1} = \lambda \cdot N_t \cdot (1 + a \cdot N_t)^{-b} - \Lambda N_t$$

where  $\Lambda = \rho \lambda$  and  $\rho$  measures the efficiency of control  $0 \leq \rho \leq 1$ . In the area bounded by  $\lambda > 1 + \Lambda$  and the upper right hand parabola populations achieve a stable equilibrium. The approach to this equilibrium may be monotonic (M) or by convergent oscillations (CO).

Equilibrium population size  $N_t = N_{t+1} = a^{-1} [(\lambda / (1 + \Lambda))^{1/b} - 1]$ .

measuring the reduction in  $\lambda$  achieved by spraying isolated plants in the crop, the equilibrium population size in the long term is calculated to be 125.8 seeds  $m^{-2}$ . Clearly this prediction under-estimates the equilibrium observed when spraying (Fig 2). (Note however the comparison is not statistically rigorous as data were collected in the same experiment!).

#### Controlling to economic threshold levels

Doyle *et al.* (1986) and Cousens *et al.* (1986) have pointed the way in using population models to calculate the long term economic benefits of alternative strategies of weed control. If an avowed management aim is to apply weed control to achieve an economic threshold weed density (determined from the relationship between yield loss and weed density at harvest, Cousens 1985), then it becomes necessary to calculate the level of control required. Stability analysis (Fig. 4) of the



appropriate model of the dynamics of the weed population provides one means, given that the model is couched in units of adult plants at harvest.

#### Evaluating the detailed effects of control measures.

Examining the fates and fluxes of individual plants at particular stages in the life cycle (eg seed  $\Rightarrow$  seedling  $\Rightarrow$  young plant  $\Rightarrow$  adult ) and constructing life tables (for example Sagar and Mortimer 1976; Lapham *et al.* 1985) has been shown to expose the importance of agricultural practices on the dynamics of weeds. Wilson and Cussans (1975) have pointed to the importance that straw burning has in the life cycle of *A. fatua* and Mortimer (1985) has illustrated the density dependent survivorship of *Eromus sterilis* seedlings under a herbicide. It is only by detailed comparative analysis in the appropriate way (k-factor analysis) that the relative importance of regulatory agents can be fully examined.

### CONCLUDING REMARKS

#### Forecasting and integrated weed management

Weed management programmes may be considered strategic in the sense that chemical and cultural measures are utilised with the foreknowledge that damage due to weeds will occur within a defined range. Moreover weed control should be practised to maximise the economic return from its application (Elliott 1982). Achieving this goal however requires precise knowledge of the damage done by weeds and the long term behaviour of the weed population. Increasingly the relationships between weed infestation density and crop damage are becoming established (Cousens 1985 ; Cousens *et al.* 1985) and the population ecology of weeds (particularly grass weeds ) understood. How far then can such knowledge be used in a predictive way especially where integrated weed management is practised ? Two points need appreciation in answering this question. Firstly that the net effects of integrated weed management programmes may be seen in terms of population trajectories (eg Fig 3) and that if appropriately described mathematically, it becomes possible to examine long term outcomes. This gives the basis for strategic forecasts (see also Mortimer 1983 ; Firbank and Watkinson 1985). Such forecasting methodology is of obvious practical benefit but the precision of the analysis depends on successful modelling of weed populations with sufficient resolution. Constructing models on the basis of linking phases in the life cycle in discrete stages runs the risk of loss of precision especially when control measures interact in complex density dependent ways and may effect not only mortality of weeds but the competitive ability and fecundity of survivors. The inescapable fact that soil and climate varies, many weed species show episodic germination and show very strong yield compensation means that strategic models need to be applied in worst and best case scenarios and coupled to economic risk analysis to be of worth. This is the next challenge in the application of population ecology in weed science.

A limitation of the above approach is that it is confined to single species dynamics when in reality weeds persist in communities. Stability analysis of the form illustrated in Fig. 4 may be extended to two species interactions and the relative

competitive abilities of species in mixture assessed. (Gould and Mortimer in prep). Further extensions to multi-species assemblages are likely to prove impracticable. Developing mechanistic models (eg Spitters and Aerts 1983) may be one alternative although this constitutes a very long term endeavour.

#### Conservation in agroecosystems.

Evaluating vegetation management programmes to conserve plant species in headlands, field margins or hedgerow bottoms (the habitat islands of agroecosystems) can be approached in a similar way to that outlined above for weed control but with the converse interest in ensuring population growth rates do not fall below unity. Yet designing management programmes is complicated by the fact that the aim is to increase community diversity rather than to diminish it. Whilst alternating strip margins around fields have illustrated that diversity can be markedly increased in relatively short time (Carter 1983), knowledge of how communities will develop is considerably lacking. Detailed studies of the population ecology of individual species, in particular their dispersal characteristics, may well prove an invaluable first step in exposing the relevant factors. However, research in this area is likely to be most productive if experimental programmes investigate not only the wide range of habitats that arise from the extremely various uses to which field margins and headlands are put (Fielder 1987) but also to the direct and indirect influences of machinery passage. It is of particular importance to assess whether desirable similar habitats need to be in some way contiguous and what their relevant size should be.

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## THE USE OF WEED DENSITY - CROP YIELD RELATIONSHIPS FOR PREDICTING YIELD LOSSES IN THE FIELD

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## ABSTRACT

The merits and shortcomings of additive and replacement series experiments for investigating competition between crops and weeds are discussed. Competition between wheat and brome grass (*Bromus diandrus*) in Western Australia is used as an example to demonstrate that the results of additive experiments can be used to develop weed density - crop yield relationships which can reliably predict yield losses under different cropping conditions encountered over large regions and between seasons.

Various ways in which farmers and their advisers can use the relationships in the field as an aid when making weed control decisions are described.

The level of precision required when developing crop loss predictions for field use is questioned. A need for future work on the effect of mixtures of two or more weed species on crop yields is identified.

## INTRODUCTION

Nearly three decades have elapsed since de Wit (1960) introduced a model (replacement series) describing competition between two plant species, based on their growth in monocultures and in various ratios of mixtures at constant total density. Subsequently Baeumer and de Wit (1968) developed a simulation model to predict interference between the components of a binary mixture of plant species through time, on the basis of measurements derived from spacing experiments with the species grown in monocultures and harvested at intervals. Spitters and van den Bergh (1982) placed the Baeumer-de Wit model in a crop-weed context and described how it could be further extended to simulate the effects on crop growth and yield of weed density, time of weed emergence relative to the crop and time of weed removal from the crop.

Although the models based on the replacement series have provided a useful framework in which to consider competition between crops and weeds and have made a valuable contribution towards clarifying thinking in this field, to our knowledge the approach has not been used for predicting the effects of weeds on crops in practical farming situations. One of the reasons for this could be the lack of a biological or physiological foundation for these models. For example, Newman (1982) stated that, 'de Wit's method of analysis was derived from equations applicable to vapour and liquid phase relations of mixtures of two substances. Its application to plant interference has never, to my knowledge, been critically related to the physiological response of plants to shortage of resources'. Furthermore, de Wit (1960) lumped all the factors, for which plants might compete, under the generic term 'space' and suggested that 'to do otherwise is not necessary, always inaccurate and therefore unadvisable'. Such logic does not sit well with physiologists investigating mechanisms involved in crop-weed competition. Donald

(1963) criticised this aspect of de Wit's approach and stated that 'whilst the use of the term space may be a convenient shorthand for mass competition, it evades the need to pursue and recognise real factors for which competition is occurring'. Hall (1974) recognised this problem and suggested a way of combining a de Wit analysis with data on nutrient uptake, to define the causal factors in competition.

Spitters and van den Bergh (1982) commented on the artificiality of this and recommended dynamic simulation as an alternative but they acknowledge that their model serves solely to illustrate the use of systems analysis in weed research and for accurate predictions the model should be extended to include physiological aspects. More recently, van Heemst (1985) pointed out that 'although the behaviour of crops and weeds in mixtures can be described fairly well on the basis of their performance in monocultures, the necessary information for such a quantitative description is mostly not available, and it is more practical to use empirical relationships based on field studies'. Furthermore, simulation modelling is complex and field agronomists and advisers may distrust this 'black box' packaging of information.

There are other possible reasons for the lack of adoption of the de Wit approach. Because it is also empirical, it is not likely to decrease field experimentation required to develop and verify weed density - yield loss relationships. The data obtained from replacement experiments are not readily translated to weed problems in the field, as much of the data generated are for densities of crop and weed far outside common field occurrence. Furthermore, the practical difficulties of planting replacement experiments may outweigh the disadvantages of additive experiments.

#### ADDITIVE EXPERIMENTS

The vast majority of weed/crop experiments conducted in the past have used an additive approach. In additive experiments two species are grown together, and the density of one (usually the crop) is held constant while the other (the weed) is varied. This approximates the farm situation where crop density is set by the farmer and weeds are usually unwanted, variable additions. A further common example of an additive (or perhaps 'subtractive') experiment is where a herbicide is used to subtract weeds from a mixed crop-weed population. Information derived from additive and subtractive experiments can be brought together, and described in crop-weed competition relationships which usually take an exponential or hyperbolic shape (Cousens 1985), similar to the one presented in Fig. 1. Notable features of such a general relationship are the near linear loss of yield at low weed densities, which is often the area of commercial interest, and the plateau at high densities.

Additive experiments have been criticised because often they describe the effect of a weed on a crop at a single site/season, or at best a few sites and seasons, and because of this may have very limited predictive value, although in many cases this criticism can be levelled at replacement experiments also. The literature abounds with additive experiments which have little more than historical value and the studies of Dew (1972) and Reeves (1976) who attempted to draw general conclusions from additive experiments and use these to predict the effect of weed infestations, are exceptions. Spitters and van den Bergh (1982) have criticised additive experiments, stating their disadvantage to that there are no adequate mathematical models to quantify the competition effects

and to make predictions on various competitive situations. The analysis of Cousens (1985) suggests that this is not so. We contend that for some crop-weed combinations, additive experiments and simple mathematical procedures can be used to predict losses due to weeds over a wide range of cropping situations. The remainder of this paper describes how additive experiments involving the annual weed, Bromus diandrus and wheat, can be used to predict wheat yield losses in different cropping situations in the wheatbelt of Western Australia, an area of about 10 million hectares.

#### ADDITIVE EXPERIMENTS WITH WHEAT AND BROME GRASS

Brome grass (B. diandrus) is native to the Mediterranean region. After its introduction to Australia it spread through the temperate agricultural areas, and is now an important weed of cereal crops. Brome grass competes successfully with wheat resulting in large losses of grain yield (Gill & Blacklow, 1984). Recently Gill et al. (1987) and Poole & Gill (1987) have analysed the results of field experiments with wheat and brome grass in Western Australia. Six experiments were carried out over three years at five locations to investigate competition between wheat and different densities of brome grass. Brome grass density was measured within 4-6 weeks of planting. The trials were sown over a range of seasons, soil types and localities. Over different years and locations, the relationship between weed density and grain yield of wheat followed a similar trend. Therefore, data on grain yields were normalized and expressed as a percentage of weed free yield and an exponential curve was fitted to the data on relative grain yield (Y) of wheat and weed densities (X), using the maximum likelihood program (Ross, 1980). Different parameters of the exponential model fitted by the maximum likelihood programme are described below:

$$Y = A + B. e^{-kx}$$

where  $A + B$  = weed free yield (100% in the present case), B is an estimate of maximum yield reduction, K = a decay constant, BK is an estimate of initial rate of decrease in relative yield, X is brome grass density (plants/m<sup>2</sup>) and Y is relative grain yield (predicted).

In a recent review of models used to describe competition between crops and weeds, Cousens (1985) found that rectangular hyperbolae accounted for the greatest proportion of the variation in the data. However, Gill et al., (1987) found the exponential model to be as good as Cousens hyperbolae although the hyperbolae may offer greater flexibility. In Fig. 1(a), the data from six experiments are shown with the fitted curve. The density of brome grass accounted for 87% of the variability in the data on grain yield of wheat (Rectangular hyperbola 86%).

In Fig. 1(b) independent data of Gill and Blacklow (1984) and Gill (unpublished 1985 and 1986) are shown against the curve previously fitted. The experiment conducted in 1986 concentrated on low densities of brome grass as this, from the recommendation viewpoint, is the area of most commercial interest. There is good agreement between the fitted curve and results obtained in later years. These latter data support the contention of Cousens (1987), that rectangular hyperbolae, or in the present case, exponential relationships better describe the relationship between yield loss and weed density than the sigmoidal relationship described by Zimdahl (1980). That is, yield begins falling with the

addition of the 'first' weed, rather than Zimdahl's proposition that low densities of weeds may have no effect on yield. Although it is possible to hypothesize situations of luxury resource supply where a sigmoidal relationship could hold, this will rarely be encountered in the field. In Australia, nutrients and water commonly limit cereal growth and at the close spacing found in wheat or barley crops, the 'first' weed could be expected to capture some of these resources.

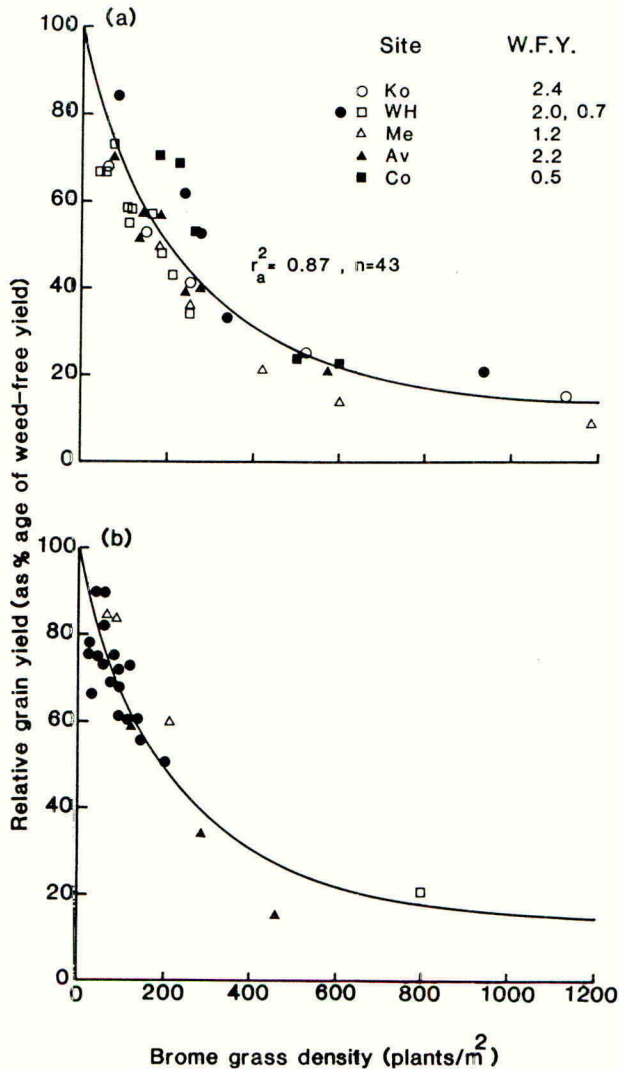


Fig. 1. Relationship between the density of brome grass and grain yield of wheat. (a) Fitted curve to our data from 6 experiments, and (b) comparison of the fitted curve with the independent results of Gill and Blacklow (1984) (□) and our trials during 1985 (▲) and 1986 (●). W.F.Y. is the weed-free yield in t/ha and  $r_a^2$  is the variability accounted for by the relationship.

## USE OF RELATIONSHIP FOR PREDICTION OF YIELD LOSS

If the relationship derived is to be used to predict losses of wheat yield at different brome grass densities, it must account for most of the cropping situations likely to be encountered. At this stage, for this combination of brome grass and wheat in Western Australia, the relationship appears remarkably robust. Experiments have been carried out over five seasons and nine sites representing a wide geographical and soil type spread. Weed free yield varied from 0.5 to 2.44 t/ha indicating the range of seasonal and edaphic conditions encountered. In view of the results obtained we are confident that, within the confines of normal cropping practices used in Western Australia, the relationship is a valuable tool for predicting yield loss for crops of different achievable yield infested with different brome grass densities. There are error terms associated with the estimates of weed density and grain yield. Therefore, it is not surprising that there is a spread of data points around the fitted curve (Fig. 1a). Some users may prefer to include a band enclosing the data spread and express a range of yield loss for a particular weed density, but this may be an unnecessary complication when using the curves with the farmers.

Many studies have reported interactions in crop-weed competitiveness between weed density and crop seeding rate, time of seeding and time of weed emergence. These were reviewed by Zimdahl (1980), Harper (1977) and Newman (1982). While it is simple to demonstrate these interactions, frequently the treatments depart so far from common farm practice for a region that they have little practical significance. Brome grass commonly germinates as a single flush with cereal crops at the start of the season (Gill and Blacklow 1984) and for this weed, time of emergence relative to the crop is not normally an important factor. With respect to changes in crop seeding rates, farmers choose seeding rate in keeping with experience and they rarely vary outside a narrow range over large regions. While it is possible to show significant interactions by doubling or tripling normal seeding rates, on the basis of cost effectiveness and deleterious side effects on lodging, water use and disease this is unlikely to be used for reducing weed competition. In summary, provided farmers continue to use normal agronomic practices in a region, the relationship derived appears very valuable for predicting losses of wheat yield due to different brome grass densities.

Will other crop-weed relationships derived in this way will show similar robustness? Elsewhere (Poole & Gill 1987), we have described a similar approach for wheat in competition with other grass weeds. Relationships were derived for three annual grasses, wild oats (*A. fatua*) barley grass (*H. leporinum*) and annual ryegrass (*L. rigidum*). For wild oats the relationship derived was satisfactory ( $r^2 = 0.95$ ) but it has only been tested in fertile, good rainfall conditions. However, when wild oat competition data from elsewhere were plotted against this relationship, in all but one case they fell on or near the curve, providing encouragement that the relationship has some generality. A complicating factor with wild oats is late emergence and it may be necessary to derive a separate relationship for this situation. Also Martin *et al.*, (1986) describe separate curves for widely separated times of planting. Given the construction of several curves, and experience with interpolation, it may be possible to use the wild oat-wheat relationship for prediction in many localities. With annual ryegrass, which has smaller seeds than wheat, it has been necessary to draw two curves, one describing ryegrass emerging with the wheat under normal



seasonal conditions, the other describing late or slow germination in seasons with a dry start. With barley grass, although we reported a good relationship (Poole & Gill, 1987), further work has suggested that soil fertility status may be important, with barley grass competing more strongly with wheat under fertile conditions.

#### USE OF COMPETITION CURVES IN THE FIELD

We have concluded elsewhere (Poole and Gill 1987) that despite the diversity of the information available it is possible to derive relationships for some important weeds which are useful when making weed management decisions under wide ranging conditions, extending at least to the regional level. It should be stressed however that estimation of crop yield loss in a particular weed situation is only part of the total assessment of the financial loss resulting from weed infestation, although it is usually the one uppermost in farmers minds when making a decision on crop spraying in the cropping year.

When evaluating yield losses derived from crop-weed competition studies, it is tempting to take the yield difference between the weed-free and the weedy situation as the value which will accrue if a control measure is invoked. This will invariably be an overestimate of the likely gains, particularly in the case of herbicides applied after crop emergence. Apart from crop damage and the reduced competitiveness which the herbicide may cause, herbicides are seldom applied early enough to prevent completely the weed reducing crop yield; the herbicide may miss some weeds; herbicides are often not fully effective and may either allow survivors or only suppress weed growth; and tolerance to herbicides may exist in the weed population. Competitive relationships will require adjustment for this in the light of experience and experiment.

Many workers have stressed the importance of assessing the value of weed control practices over time, usually emphasising the importance of weed seeds which are produced in a weedy crop carrying forward to infest crops or pastures in later years. Cousens (1987) has discussed the importance of this recently, although Marra and Carlson (1983) suggest that future benefits from carryover effects of controlling weeds in one year to later years may be so uncertain that it is best to ignore them. Auld and Tisdell (1986), however, suggest that increased uncertainty about the future may be taken into account by applying larger discounts to future costs and benefits, thereby putting a reduced weight on these in decision making. Pannell and Panetta (1986) have placed weed control in a whole farm context and using linear programming to arrive at overall cost of a weed in a farm system. The usefulness of these models depends greatly on the data entered into them. Reasonably accurate estimates of the effects of weeds on crops may be the most important data entered and this appears to be the case in the Pannell-Panetta model.

Firstly, we agree with Cousens (1987) who describes the various 'weed thresholds' used in the literature, that a single critical or threshold density for action has little validity outside a very narrow range of conditions. It is clear from the weed density - yield relationship presented earlier in this paper that for a particular brome grass density, the yield loss will vary greatly depending on the crop size. For example for a density of 100 brome grass plants/m<sup>2</sup>, the yield loss for crops with potential yields of 1, 2 and 3 tonne/ha is 300, 600 and 900 kg/ha respectively. A farmer confronted with 100 brome grass plants

in a one tonne crop might make a very different weed control decision to one with a similar density in a three tonne crop.

Experience with farmers and advisers suggests that rather than presenting a fixed critical density, it is more useful, and enlightening, to present data in a way which allows the farmer to gain an idea of the sensitivity of crops of different size to different brome grass densities. Then, even if the farmer is not sure about his likely final yield, or his brome grass density, he can 'cast around' and rapidly gain an appreciation of the sensitivity of the grain losses he will sustain in different size crops infested with different brome grass densities. To allow farmers to do this readily, the information contained in the exponential function described has been presented to them in three ways. This, in itself, allows users to choose the package with which they are most comfortable.

#### Two-way tables

In Table 1 the information has been placed in a two way table, which shows the likely grain loss for different crops, in this case covering the normal range of yields and brome densities found in Western Australia. The table has been filled out in the lower density range as it is here that most difficulty is found when making weed control decisions. The information can also be presented as monetary loss for a given wheat price, or actual yield achieved. Even if the farmer has only a vague idea of his yield potential and brome grass population, he will usually have a firm cost for a control measure, which he can place against the table, and arrive at combinations of crop size and weed density where it will pay to intervene.

Table 1. Wheat grain yield loss caused by brome grass at different densities in crops of different weed-free yield potentials

Potential weed-free yield (kg ha <sup>-1</sup> )	Brome grass weed density (plants m <sup>-2</sup> )					
	25	50	100	200	300	400
750	67	127	225	367	457	517
1000	90	170	300	490	610	690
1500	135	255	450	735	915	1035
2000	180	340	600	980	1220	1380
3000	270	510	900	1470	1830	2070

These tables allow the farmer to appreciate the impact of brome grass at different densities, and although he may not be able to define his problem further than 'a few' or 'a lot' of brome, or 'one brome for each wheat plant' he can gain an appreciation of likely losses. A single 'critical density' figure does not allow this. In terms of long term weed management, the table may show him that applying a control practice may result in a profit, break-even or loss in that crop, but he can place a judgement on whether to proceed with a practice which will minimise future problems.

Weed cost ready reckoners

The relationships derived have also been placed in ready reckoners (Burgess and Gill 1986) which allow the same 'casting around' as the two way tables, but include different wheat prices also. This method of presentation is shown in Fig. 2. These charts and the tables can be used in the field.

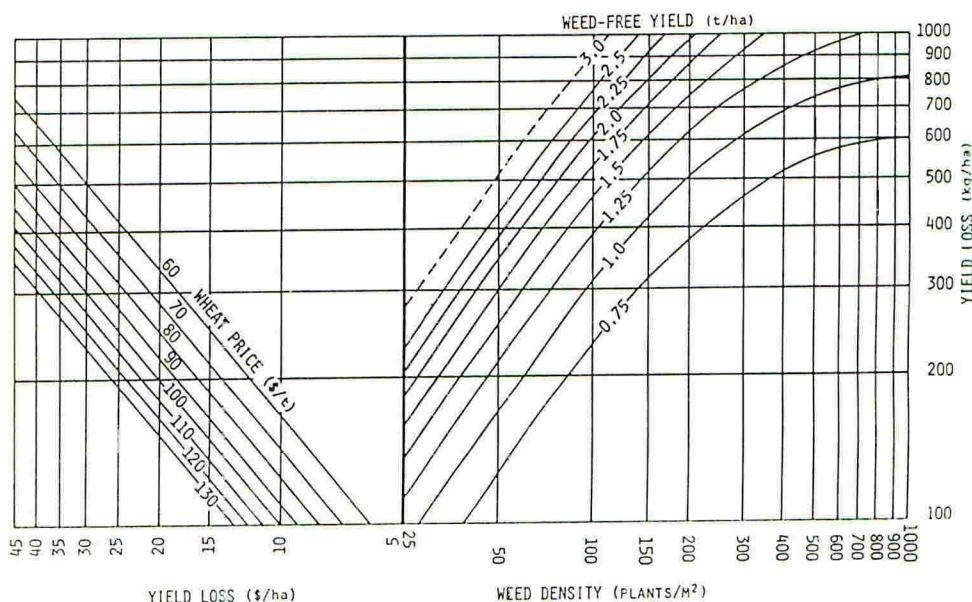


Fig. 2. The 'Weedcost' ready reckoner for brome grass in wheat.

Computer printout

The information has also been programmed for use in microcomputers. The computer prompts the operator with what weed? what weed density? what crop potential? what crop price? and immediately shows losses in kilograms/ha and \$/ha. Again, the farmer can rapidly 'cast around' to help his decision making.

Expert systems

The next step, which is in train at present, is to incorporate the relationships within the framework of expert systems technology which will allow farmers to quiz the system about weed control options.

## COMMENT

The use of weed density to predict losses due to weeds in crops has been criticized on two grounds. The first is that it is difficult and time consuming to measure (Cousens 1987) and the second that it has limited biological significance, for biomass and leaf area rather than weed density are the key factors which determine uptake of nutrients and water and interception of radiation by a plant species. In this paper we have attempted to show that weed density, measured within 4-6 weeks of

crop emergence, correlates well with yield loss, and can be used to predict crop loss over large agricultural regions and across seasons, provided agronomic practices stay within the range normally used in the region. The difficulty of measurement is acknowledged, as is the variation in density across fields. However, weed density is more easily estimated than weed biomass. Also, when decisions on control practices are made, soon after crop emergence, measurement of biomass of weed seedlings may have little relevance. Gill (1986 unpublished) has shown good correlation between early weed seedling counts and final biomass.

Many workers have shown that weeds which emerge later than a month after the crop emergence have little effect on crop yield, and contribute little to seed production by weeds in the crop. This supports the use of early weed counts for estimates of crop loss. It is acknowledged that for some weed situations, for example where a weed causes tainting, harvesting difficulties or grain contamination, low weed densities and late emerging plants assume importance, and the effect of weeds on yield may then be a secondary consideration.

This paper has not addressed the common problem of mixed weed populations in crops. The impact of controlling one weed species on the competitive relationship of the remaining weeds and crop has been raised by Haizel and Harper (1973), Spitters and van den Bergh (1982) and Poole and Gill (1987). This problem needs to be addressed urgently and is the subject of a present study.

A question which arises when constructing weed competition models is how far to refine them. The spectrum of 'models' available ranges from a single critical weed density figure to complete specification of a physiologically based model (Rijsdijk 1986). The construction of physiological models is difficult and at present may involve so many assumptions that the output is questionable. The models we have described, while being far from satisfying because of their empiricism, are simple mathematically, can be constructed from a combination of historical and easily acquired data, are readily verified under field conditions, are quite robust, and may be all that a farmer wants to help him with his weed control decisions.

While not wishing to diminish the value of simulation or mechanistic modelling, the resources are simply not available to construct such models for even the major crop-weed combinations in an agricultural region. The specification of a model which is sufficiently general to account for most crop-weed situations, yet at the same time has an output which is precise and simple to use in the field appears to be a long way off. It is possible that the two goals are incompatible.

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## THE EFFECT OF WEED INTERFERENCE ON THE GROWTH AND YIELD OF WHEAT

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## ABSTRACT

The relative competitiveness of *Avena fatua*, *Alopecurus myosuroides* and *Stellaria media* with winter wheat cv. Norman (*Triticum aestivum*) was compared under uniform glasshouse conditions. Each weed was grown at a range of densities equivalent to 0, 20, 40, 80 and 160 plants/m<sup>2</sup>. Weed interference reduced wheat grain yield mainly through a decline in the number of fertile tillers per pot. The order of competitiveness seemed to be *A. fatua* > *A. myosuroides* > *S. media*. The losses in terms of wheat grain yield loss varied in the ranges 27% to 72%, 0.3% to 56% and 0.3% to 32% respectively for the lowest to highest densities of *A. fatua*, *A. myosuroides* and *S. media*. Linear and non-linear models of yield loss-weed density relationship are compared for each weed species.

## INTRODUCTION

Wild-oat (*Avena fatua*) and black-grass (*Alopecurus myosuroides*) are two major grass weeds in cereals (Phillipson 1974, Elliott *et al.* 1979). *A. fatua* can cause large yield losses in winter cereals (Wilson & Cussans 1978). Interference from *A. myosuroides* can also cause serious yield losses in cereals (Naylor 1972, Moss 1980). Common chickweed (*Stellaria media*) is one of the most widespread cereal weeds, although considered to be less troublesome than grass weeds (Mann & Barnes 1950). There is however usually a significant yield response to the control of *S. media* in winter barley (eg. Orson 1980).

In the study we compare directly the effects of varied densities of *A. fatua*, *A. myosuroides* and *S. media* on the growth and yield of winter wheat cv. Norman. The data are used to evaluate the relative losses due to different weeds, and to test differing models of the yield loss - weed density relationship.

## MATERIALS AND METHODS

Additive experiments were carried out under glasshouse conditions (20 ± 6°C; 16 h supplementary lighting). Plants were grown in 25 cm diameter plastic pots with bottom drainage in a sandy loam:peat moss mixture (80:20). Three uniformly pre-germinated seeds of the crop or weed were sown in each position, in a pre-set regular pattern, in the pots. Seedlings were thinned to the required numbers one week after emergence. Standard fertilizers were applied at rates equivalent to 80:60:45 kg/ha N:P:K one week before sowing. Four additional N dressings were applied at rates equivalent to 30, 20, 20 and 10 kg N/ha at tillering (GS 21:Zadoks *et al.* 1974), stem elongation (GS 30), booting (GS 40) and end of anthesis (GS 70) of wheat plants.

A randomised complete block design with 3 replications was used. A constant density of eight wheat plants per pot was established. Weed

densities were 0, 1, 2, 4 and 8 *A. fatua*, *A. myosuroides* or *S. media* plants per pot, equivalent to 0, 20, 40, 80 and 160 plants/m<sup>2</sup>.

The grain yield of both crop and weed plants were harvested at 26-29 weeks after sowing, as they reached maturity. Plant height, number of tillers, number and length of ears, and dry weights of shoots were determined. The ears were threshed: number of grains per ear, and dry weights of chaff and grain were recorded. Data were subjected to analysis of variance using the program Genstat. The data were used to test linear (Dew 1972, Carlson *et al.* 1981) and non-linear (Wilson & Cussans 1983, Cousens *et al.* 1984, Cousens 1985) models of the yield loss - weed density relationship. The models were fitted using the program BMDP.

## RESULTS

### 1. Biomass production

The total dry matter yields (as % of plant biomass present in controls) of winter wheat cv. Norman and crop + weed are shown in Fig. 1.

No significant difference (comparisons based on actual yield data) was observed in total biomass production (crop + weed) as the density of *A. myosuroides* or *S. media* increased, although it appeared to be slightly lower than that of weed-free control. *Avena fatua* reduced the dry weight biomass of wheat. The percentage dry weight reduction was significantly more than was caused by the other two weed species. Although there was no significant difference between *A. myosuroides* and *S. media*, there is an indication in Fig. 1 of a more rapid rate of yield loss, with increasing weed density, for the grass weed. Total dry matter production by *A. fatua* was always higher than that of either *A. myosuroides* or *S. media*: there was no difference between the latter two species.

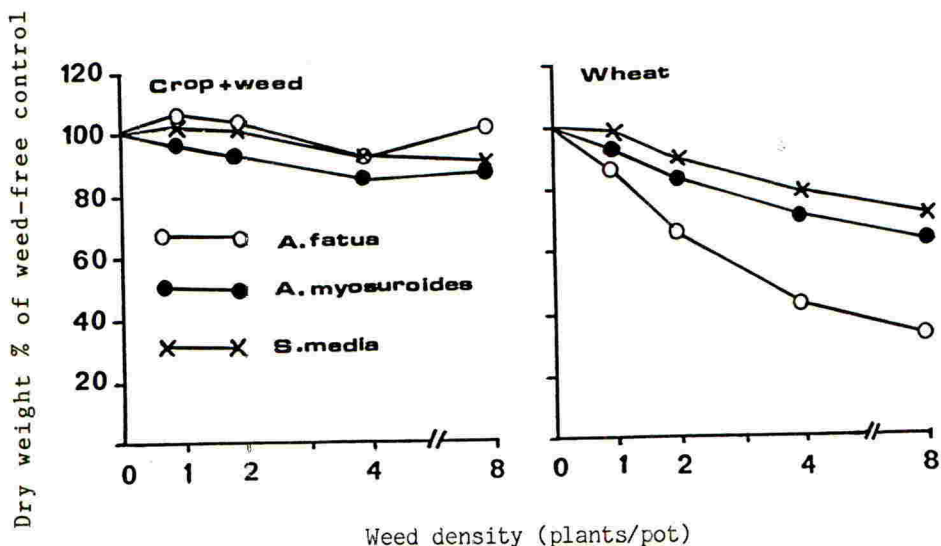


Fig. 1 The effect of different weed species on total dry matter production (crop + weed) and wheat dry weight.

## II. Yield and its components

The effects of increasing density of different weeds on wheat grain yield and its components are shown in Table 1.

Grain yield was reduced by increasing weed density. The loss of crop yield was mainly due to a reduction in fertile tiller number. Number of grains per ear, and kernel weight, were also reduced by the presence of weeds in most cases, but to a lesser extent. The greatest yield reduction occurred in *A. fatua* pots. The results of this experiment showed the order of competitiveness to wheat to be *A. fatua* > *A. myosuroides* > *S. media*. The losses in terms of wheat grain yield varied from 27% to 72%, 0.3% to 56% and 0.3% to 32% respectively, for the lowest to highest densities of *A. fatua*, *A. myosuroides* and *S. media*. Wheat dry weight was not reduced to the same extent as grain yield. The losses from these three weeds, in terms of crop total dry weight, respectively varied from 12% to 67%, 5.8% to 37% and 3% to 29% for the lowest to highest weed densities.

TABLE 1

Wheat grain yield and yield components as influenced by different weed species (mean of n = 3 replications; each control replicate taken as the mean of two weed-free control pots)

	Weed density plants/ pot	Grain yield g/pot	No. of ears/ plant	No. of grains/ ear	Kernel weight mg
Weed-free control	0	10.70	1.97	26.60	25.1
<i>Avena fatua</i>	1	7.77	1.57	25.7	23.8
	2	6.43	1.37	26.50	23.0
	4	5.20	1.13	25.10	23.1
	8	2.97	1.00	17.70	21.4
<i>Alopecurus myosuroides</i>	1	10.67	1.93	26.33	25.9
	2	8.37	1.47	26.30	24.5
	4	6.03	1.33	23.80	23.8
	8	4.67	1.17	23.20	20.8
<i>Stellaria media</i>	1	10.67	1.97	26.63	25.5
	2	9.73	1.80	26.57	24.2
	4	9.40	1.80	25.9	24.7
	8	7.20	1.60	23.60	24.1
SE	-	0.57	0.14	1.69	0.67

The goodness of fit of each of the six models to the observed data in terms of residual sum of squared (R.S.S.) varied between the three species (Table 2). For *A. fatua* the best fit was given by the linear model 2 (square root of weed density), with model 6 (non-linear hyperbolic) also giving a very good fit. Only the simplest model (1:linear) gave a poor fit



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TABLE 2

Residual sum of squares (R.S.S.) for linear and non-linear models fitted to wheat grain yield loss data.

Weed species	<u>A. fatua</u>	<u>A. myosuroides</u>	<u>S. media</u>
Model	R.S.S.	R.S.S.	R.S.S.
1. $Y_L = Id$ Thurlow & Buchanan (1972)	1233	1296	317
2. $Y_L = b_1 \sqrt{d}$ Dew (1972)	112	1408	608
3. $Y_L = b_1 \sqrt{p}$ Carlson <u>et al.</u> (1981)	241	2035	930
4. $Y_L = Ip + cp^2$ Carlson <u>et al.</u> (1981)	213	903	313
5. $Y_L = A(1 - \exp(-Id/A))$ Wilson & Cussans (1983)	235	965	374
6. $Y_L = Id/(1 + Id/A)$ Cousens (1985)	169	1075	422

d = density  
 p = weed density/(weed density + crop density)  
 b<sub>1</sub> = regression coefficient = index of competition as defined by Dew (1972)  
 I = initial % yield loss  
 A = asymptotic % yield loss  
 Y<sub>L</sub> = yield loss

TABLE 3

Competitiveness of different weed species with wheat as expressed by initial % yield loss (I)

Weed species	I % per plant/pot	index of competitiveness compared with <u>A. fatua</u>
<u>A. fatua</u>	33.8	1.00
<u>A. myosuroides</u>	15.2	0.45
<u>S. media</u>	5.0	0.15

to these data. The observed data for *A. myosuroides* best described the quadratic model (4), with the two non-linear models (5,6) also giving a relatively good fit. In the case of *S. media*, again the best fit was provided by model 4, with the simplest linear model (1), and the two non-linear models also giving a good fit to the observed data. The non-linear models were closely similar in terms of goodness of fit for all three data sets. The results of curve-fitting for the hyperbolic model are shown in Fig. 2.

The comparative low-density competitiveness of the three weed species is shown in Table 3. *Avena fatua* was at least twice as competitive as the other weeds at low densities.

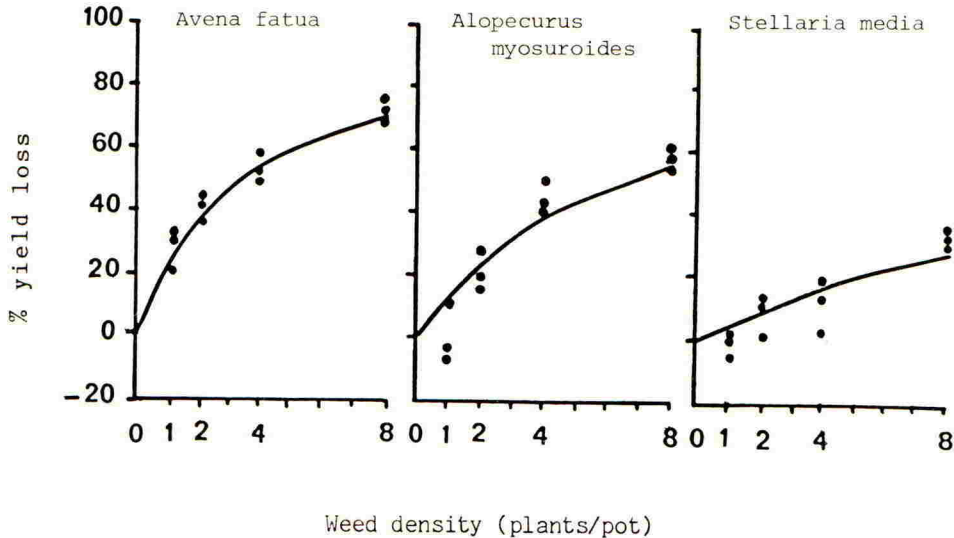


Fig. 2. The results of hyperbolic model (Cousens 1985) applied to different weed species in wheat.

## DISCUSSION

The main interference effects of *A. fatua*, *A. myosuroides* and *S. media* on wheat yield were seen in a reduced number of fertile tillers. This accords with long standing observations (e.g. Blackman & Templeman 1938, Aspinall & Milthrope 1959, Wilson & Peters 1982). *A. fatua* was the most and *S. media* the least competitive under the conditions of this trial. Shoot interference could occur due to the shading effects of tall-growing *A. fatua* plants. Willey & Halliday (1971) showed that grain yield was reduced by severe shading as the seed is being filled. The low growth habit of the other two species may reduce the importance of shoot interference with the crop. Other mechanisms, involving root-interference, probably contribute to the severe yield reduction of wheat caused by *A. myosuroides* at the highest densities and the smaller yield losses caused by *S. media*. Wellbank (1963) and Naylor (1972) for example have suggested

that A. myosuroides is a good competitor with wheat for nitrogen. However, there are insufficient data to allow conclusions to be drawn here on the differential importance of shoot v. root interference.

Dew's index of competition (Dew 1972) was found to be a good index for comparing the competitiveness of the three weed species. The index of competition for our data was found to be higher than values reported elsewhere, at 5.15, 4.12, and 2.15 for A. fatua, A. myosuroides and S. media, respectively. The index of competition for wild oats in wheat under field conditions is reported to be 3.39 (Dew, 1972) and 4.73 (Carlson & Hill 1985).

In fitting the different models to the observed data, there was no benefit from using relative weed density (p) rather than density (d) itself. This does not agree with the results of Carlson et al. (1981) and Carlson & Hill (1985) who found a better fit resulted from the use of relative proportion of wild oats in the total crop + weed stand. However we used a constant density of crop plants rather than the varying densities of wheat used by these authors.

In general the non-linear models (models 5, 6: Table 2) and Carlson quadratic model (model 4: Table 2) provided a good fit to our observed data. However the simpler linear models could also provide a good fit in certain cases (eg. model 2 and 3 for A. fatua, and model 1 for S. media). The parameter I (initial % yield loss) derived from the non-linear hyperbolic model is perhaps a rather better means of assessing weed competitiveness at low densities (i.e. before intraspecific competition effects come into play). This index has previously shown A. myosuroides to be only 1/4 to 1/5 as competitive as A. fatua according to Cousens (pers. comm.) whilst we found A. myosuroides to be nearly half as competitive as A. fatua, in terms of I, under glasshouse conditions.

#### ACKNOWLEDGMENT

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**INTERSPECIFIC COMPETITION BETWEEN THREE GRAMINACEOUS  
WEED SPECIES AND WHEAT**

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**ABSTRACT**

Binary mixtures of wild oats (*Avena fatua*), bromegrass (*Bromus diandrus*) and ryegrass (*Lolium rigidum*) were studied with respect to their effect on the growth and yield of wheat. For each weed species combination, wheat was grown with weed populations of three different total densities. At each density the weed pairs were present in five proportions. There was no evidence in the results that the weeds were interacting in a manner which modified the effect of the individual species on wheat. Comparing the individual species on a per plant basis, annual ryegrass had less effect on wheat than did bromegrass or wild oats. The resulting differences in the behaviour of the weed pairs is discussed.

**INTRODUCTION**

Wild oats (*Avena fatua*) and annual ryegrass (*Lolium rigidum*) are serious and widespread weeds of cereal crops in Western Australia (Paterson 1969, Pearce and Holmes 1976) while bromegrass (*Bromus diandrus*) is a weed of increasing significance (Holmes 1982, Poole et al. 1986).

A substantial body of information has been compiled regarding the effect on crops of many individual weed species. Such information is important for an economically sound approach to weed control. A number of authors (Moore 1971, Quinlivan 1972, Ennis 1977, Zimdahl 1980 and Gill and Blacklow 1984) have emphasised that in order to improve both the decision making processes involved in, and the efficiency of, weed control a greater knowledge is required of weed biology and the systems of which weeds are a part.

A plant responds to the totality of its environment. The resources available to a given plant are modified by the presence of neighbouring plants which thus constitute a component of the plant's environment. It should not be assumed, therefore, that the growth of a weed and its impact on a crop is independent of the presence of other weed species. Little is known of the influence of weeds on each other or the effect on a crop of a population consisting of a mixture of weeds.

The experiments presented in this paper form part of a study to investigate the interactions among the component species of plant systems which involve wheat grown in the presence of binary mixtures of wild oats, bromegrass and ryegrass. The effect of the weed species on each other and the effect of the mixed weed population on wheat is studied.

The specific aim of the experiments was to determine how the total weed density modifies the interaction between the weed species and between the crop and the weed population. The results presented are for the effect of weed density and proportion on the growth of wheat.

## MATERIALS AND METHODS

A set of three experiments was conducted at the School of Agriculture Field Station at Floreat Park, Perth, Western Australia (31°57'S, 115°47'E). The soil was a yellow sand which had been ameliorated by the addition of loam.

To enable the control of moisture, the plots were covered with polythene tunnel houses. Conditions were monitored using thermohygrographs in Stevenson screens within each house and at two adjacent points outside. Rain gauges were installed in each house and irrigation was applied using a sprinkler system. A total of 320mm of water was applied.

Each experiment comprised wheat grown with one of the three binary combinations of wild oats, brome grass and ryegrass. At each of three total weed densities, replacement series (de Wit 1960) of five proportions were used to investigate the effects of changing the proportion of the mixtures of two weed species on the growth of wheat. The treatment structure was a three x five factorial of total weed density and proportion.

The densities and proportions for all weed pairs were:

Density : 200, 400, 600 plants/m<sup>2</sup>  
 Proportion (as percentage) : 100, 75/25, 50/50, 25/75, 100

Wheat (cv. Gamenya) was present in all plots at a density of 150 plants/m<sup>2</sup>. Plots were 1.5m x 1m and contained six rows of wheat. The experimental design was a randomised complete block with two blocks.

The experiment was sown on 24 May 1985. All plots were sampled when the wheat reached anthesis and grain maturity (95 and 197 days after sowing). At each sampling four plants of each species were taken using the two central rows of wheat and the surrounding inter-rows for the weeds. The plants were cut just below ground level and morphological traits measured. The plants were then dried to constant weight at 80°C and weighed.

Transformations were used on the data to stabilize variance: natural logarithms for heights and weights and square roots for counts. The results presented in the tables are back transformed means with transformed data in parentheses. All standard errors are for the difference between transformed means. As this study was of the effect of binary mixtures of weeds on a constant density of wheat, the de Wit forms of analysis were considered inappropriate. All results reported are of wheat. Trends noted in the results are significant at least at the P = 0.05 level. All linear measurements were in mm, dry weight in mg and grain weights per plant in g.

## RESULTS

Anthesis

At anthesis the effect of the weeds on wheat growth had become evident.

Both leaf area and plant dry weight were linearly reduced by total density of ryegrass/wild oat combinations. There were no significant main effects of proportion (Tables 1 and 2). The wild oat/brome grass mixture gave no significant results (Tables 3 and 4).

TABLE 1

The effect of total weed density on wheat characteristics at anthesis for mixtures of wild oats and ryegrass.

Total Density	200		400		600		S.E.
Plant Height (mm)	745	(6.613)	726	(6.587)	668	(6.504)	0.0558
Inflorescence No	1.97	(1.2141)	0.95	(1.2034)	0.95	(1.2034)	0.0200
Dry Weight (mg)	7879	(8.972)	7624	(8.939)	6015	(8.702)	0.1239
Leaf Area (cm <sup>2</sup> )	91.9	(4.521)	84.9	(4.441)	68.0	(4.220)	0.0912

TABLE 2

The effect of the proportion of wild oats and ryegrass in the weed population on characters of wheat at anthesis.

Proportion	W.O.				R.G.		S.E.
	100%	75/25	50/50	25/75	100%		
Plant Height (mm)	722	718	686	700	735		
	(6.582)	(6.577)	(6.531)	(6.551)	(6.600)		0.0720
Inflorescence No	0.96	0.96	0.96	1.00	0.91		
	(1.2070)	(1.2070)	(1.2070)	(1.2247)	(1.1892)		0.0258
Dry Weight (mg)	7052	6761	6393	7809	7708		
	(8.861)	(8.819)	(8.763)	(8.963)	(8.950)		0.1599
Leaf Area (cm <sup>2</sup> )	72.9	87.0	84.6	82.8	78.4		
	(4.289)	(4.466)	(4.438)	(4.416)	(4.362)		0.1178

TABLE 3

The effect of total weed density on wheat characteristics at anthesis for mixtures of bromegrass and wild oats.

Total Density	200		400		600		S.E.
Plant Height (mm)	701	(6.553)	736	(6.601)	706	(6.559)	0.0277
Inflorescence No	1.12	(1.272)	1.03	(1.238)	1.05	(1.244)	0.0296
Dry Weight (mg)	8383	(9.034)	6708	(8.811)	8119	(9.002)	0.0774
Leaf Area (cm <sup>2</sup> )	66.7	(4.200)	64.6	(4.168)	63.6	(4.153)	0.1038

TABLE 4

The effect of the proportion of bromegrass and wild oats in the weed population on characters of wheat at anthesis.

Proportion	Brome				W.O.		S.E.
	100%	75/25	50/50	25/75	100%		
Plant Height (mm)	699	702	705	745	721		
	(6.549)	(6.554)	(6.558)	(6.613)	(6.580)		0.0357
Inflorescence No	1.00	1.08	1.09	1.00	1.16		
	(1.225)	(1.257)	(1.262)	(1.225)	(1.287)		0.0382
Dry Weight (mg)	8267	7639	6967	7428	8283		
	(9.020)	(8.941)	(8.849)	(8.913)	(9.022)		0.1000
Leaf Area (cm <sup>2</sup> )	61.81	63.05	60.58	74.37	65.89		
	(4.124)	(4.144)	(4.104)	(4.309)	(4.188)		0.1340

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Plant height, plant dry weight and leaf area exhibited significant responses in the ryegrass/bromegrass set. The overall weed density reduced plant height. Proportion also affected this variate; there was a linear reduction in height as the proportion of bromegrass increased. There was a significant linear reduction in plant dry weight and leaf area as the proportion of bromegrass increased, but for these variates there was no density effect (Tables 5 and 6).

TABLE 5

The effect of total weed density on wheat characteristics at anthesis for mixtures of ryegrass and bromegrass.

Total Density	200		400		600		S.E.
Plant Height (mm)	718	(6.576)	666	(6.501)	638	(6.458)	0.0262
Inflorescence No	0.97	(1.214)	1.00	(1.225)	0.99	(1.221)	0.0256
Dry Weight (mg)	6355	(8.757)	5914	(8.685)	4434	(8.397)	0.1425
Leaf Area (cm <sup>2</sup> )	66.09	(4.191)	61.13	(4.113)	48.52	(3.882)	0.1272

TABLE 6

The effect of the proportion of ryegrass and bromegrass in the weed population on the characters of wheat at anthesis.

Proportion	R.G.				Brome		S.E.
	100%	75/25	50/50	25/75	100%		
Plant Height (mm)	696	723	654	672	624		0.0338
	(6.545)	(6.584)	(6.483)	(6.510)	(6.436)		
Inflorescence No	0.91	0.96	1.00	1.00	1.08		0.0330
	(1.187)	(1.207)	(1.225)	(1.225)	(1.256)		
Dry Weight (mg)	6336	6267	5872	4675	4619		0.1839
	(8.754)	(8.743)	(8.678)	(8.450)	(8.438)		
Leaf Area (cm <sup>2</sup> )	72.24	70.11	53.30	47.66	51.37		0.1643
	(4.280)	(4.250)	(3.976)	(3.864)	(3.939)		

### Grain Maturity

At this stage the wild oat/ryegrass mixture produced a linear density effect in which wheat growth as measured by dry weight, grain number and grain yield per plant all decreased as density increased (Table 7). The dry weight, number of ears and number of spikelets per plant all increased with a decrease in the proportion of wild oats (Table 8). As expected from the anthesis results there were no significant effects due to the wild oat/bromegrass mixtures (Tables 9 and 10).



TABLE 7

The effect of total weed density on wheat characteristics at grain maturity for mixtures of wild oats and ryegrass.

Total Density	200	400	600	S.E.
Inflorescence No	1.12 (1.2731)	1.02 (1.2346)	1.05 (1.2444)	0.0214
Spikelet No	21.54 (4.641)	18.99 (4.358)	18.77 (4.333)	0.1700
Dry Weight (mg)	15788 (9.668)	13521 (9.512)	11814 (9.377)	0.1189
Grain Number	42.00 (6.481)	38.42 (6.198)	35.21 (5.934)	0.2264
Grain Weight (g)	1.757 (1.014)	1.659 (0.978)	1.385 (0.869)	0.0493

TABLE 8

The effect of the proportion of wild oats and ryegrass in the weed population on characters of wheat at grain maturity.

Proportion	R.G. 100%	75/25	50/50	25/75	Brome 100%	S.E.
Inflorescence No	1.00 (1.2247)	1.04 (1.2411)	1.04 (1.2411)	1.08 (1.2575)	1.16 (1.2890)	0.0277
Spikelet Number	18.27 (4.274)	19.24 (4.386)	18.58 (4.311)	20.07 (4.480)	22.74 (4.769)	0.2194
Dry Weight (mg)	11316 (9.334)	13575 (9.516)	12016 (9.394)	14958 (9.613)	16916 (9.736)	0.1534
Grain Number	35.74 (5.978)	39.78 (6.307)	37.52 (6.126)	38.19 (6.180)	41.34 (6.430)	0.2922
Grain Weight (g)	1.421 (0.884)	1.675 (0.984)	1.535 (0.930)	1.581 (0.948)	1.779 (1.022)	0.0636

TABLE 9

The effect of total weed density on wheat characteristics at grain maturity for mixtures of brome grass and wild oats.

Total Density	200	400	600	S.E.
Inflorescence No	1.05 (1.244)	1.07 (1.252)	1.10 (1.264)	0.0279
Spikelet Number	19.96 (4.468)	19.94 (4.465)	21.09 (4.592)	0.1584
Dry Weight (mg)	12283 (9.416)	12052 (9.397)	11873 (9.382)	0.0867
Grain Number	34.02 (5.833)	33.20 (5.762)	33.17 (5.759)	0.2289
Grain Weight (g)	1.428 (0.887)	1.312 (0.838)	1.323 (0.843)	0.0490

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TABLE 10

The effect of the proportion of brome grass and wild oats in the weed populations on characters of wheat at grain maturity.

Proportion	Brome				W.O.	S.E.
	100%	75/25	50/50	25/75	100%	
Inflorescence No	1.16 (1.287)	1.00 (1.225)	1.04 (1.241)	1.04 (1.241)	1.12 (1.274)	0.0361
Spikelet Number	21.95 (4.685)	18.91 (4.349)	19.64 (4.432)	19.83 (4.453)	21.37 (4.623)	0.2045
Dry Weight (mg)	11920 (9.386)	11362 (9.338)	11992 (9.392)	12991 (9.472)	12137 (9.404)	0.1119
Grain Number	31.40 (5.604)	32.99 (5.744)	32.58 (5.708)	37.70 (6.140)	32.81 (5.728)	0.2955
Grain Weight (g)	1.237 (0.805)	1.363 (0.860)	1.303 (0.834)	1.545 (0.934)	1.333 (0.847)	0.0633

There was a linear response to density in the ryegrass/brome grass series for dry weight and spikelet number. In both cases increased density decreased the yield. There was no significant effect of proportion (Tables 11 and 12).

TABLE 11

The effect of total weed density on wheat characteristics at grain maturity for mixtures of ryegrass and brome grass.

Total Density	200	400	600	S.E.
Inflorescence No	1.02 (1.2346)	1.05 (1.2451)	1.00 (1.2247)	0.0083
Spikelet Number	18.41 (4.291)	18.75 (4.330)	16.54 (4.067)	0.0789
Dry Weight (mg)	12657 (9.446)	11920 (9.386)	9396 (9.148)	0.1279
Grain Number	35.05 (5.92)	32.26 (5.68)	28.52 (5.34)	0.3720
Grain Weight (g)	1.370 (0.863)	1.330 (0.846)	1.119 (0.751)	0.0774

TABLE 12

The effect of the proportion of ryegrass and brome grass in the weed population on characters of wheat at grain maturity.

Proportion	RG				Brome	S.E.
	100%	75/25	50/50	25/75	100%	
Inflorescence No	1.00 (1.2247)	1.08 (1.2575)	1.04 (1.2411)	1.00 (1.2259)	1.00 (1.2247)	0.0107
Spikelet Number	17.56 (4.190)	19.56 (4.423)	18.02 (4.245)	16.44 (4.055)	17.91 (4.232)	0.1018
Dry Weight (mg)	11441 (9.345)	14750 (9.599)	11004 (9.306)	8875 (9.091)	10862 (9.293)	0.1651
Grain Number	34.11 (5.84)	34.69 (5.89)	31.02 (5.57)	27.67 (5.26)	32.15 (5.67)	0.4810
Grain Weight (g)	1.396 (0.874)	1.455 (0.898)	1.223 (0.799)	0.994 (0.690)	1.312 (0.838)	0.0999

## DISCUSSION

The results of studies on the interaction of annual ryegrass and wheat (Reeves 1976 and Rerkasem *et al.* 1980) led to the expectation that, in the present experiments, at least ryegrass would have had a deleterious effect on wheat growth and yield. There is evidence that similar expectations would apply to wild oats and brome grass (McNamara 1972, Paterson 1969 and Poole *et al.* 1986).

As expected, the total density of the weeds reduced wheat growth and yield. Over the range considered, the effect was proportional to the number of weeds present. These results applied to wild oat/ryegrass and ryegrass/brome grass mixtures only. The wild oat/brome grass mixture had no significant effect on wheat.

Information on the respective competitive status of these three species of weed against wheat derives from the effect of the proportions. Wild oats had a greater impact on wheat than did the ryegrass in the wild oat/ryegrass experiment while brome grass did not differ significantly from either ryegrass or wild oats. It is concluded that in these binary mixtures ryegrass is the least competitive species against wheat followed by brome grass and wild oats; the relative status of these two is unclear.

In the brome grass/wild oat experiment no effect of total density was found. Results for both the effect of wild oats (Paterson 1969) and brome grass (Poole *et al.* 1986) on wheat in Western Australia indicated that the greatest effect of these two weeds occurred at low densities. McNamara (1972) states that in New South Wales the maximum effect of wild oats is attained at a density of 300 plants/m<sup>2</sup>. The results of the current study support these findings in that the absence of a significant effect of densities above 200 plants/m<sup>2</sup> (the minimum density used) suggests that these densities are in the flatter part of the response curve to these weed species. By contrast, Reeves (1976), working in Victoria, found a response of wheat yield to ryegrass density which had a more constant gradient over a wide range of densities; this would account for our results when ryegrass is present.

The results discussed with respect to wheat growth appear general, with plant height, dry weight, leaf area and at grain maturity, grain variates being influenced by the weeds in the manner described.

There was little indication that the weeds interacted in a manner which modified the effect of the individual species on wheat. If this had been the case one would have expected marked deviations from the linear trends of proportions within the replacement series.

Further work is in progress to confirm these results and to study the implications for crop growth.

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## RELATIVE TIME OF EMERGENCE, LEAF AREA DEVELOPMENT AND PLANT HEIGHT AS MAJOR FACTORS IN CROP-WEED COMPETITION

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## ABSTRACT

Growth analysis data (dry weight, LAI and height) are presented of competition experiments with sugar beet (Beta vulgaris cv. monohill and cv. salohill), Fat hen (Chenopodium album) and Chickweed (Stellaria media), as well as with beet and early and later sown Chenopodium. Yield losses are not related to leaf area, the worst weed Chenopodium having the lower LAI. The paradox is explained by different height growth of the weed species in view of the competition for light.

A time lag of 21 days between the emergence of crop and Chenopodium still leads to yield losses; weeds emerging 30 days later than the crop no longer develop a canopy on top of the crop's and no longer lower yields.

## INTRODUCTION

In open and early sown crops such as sugar beet, a group of late summer annuals tends to escape the current mechanical operations and even soil herbicides; mechanical control measures during early crop growth may only be effective between the rows. Remaining weeds in the row, even at low density, often cause substantial damage (Solanum nigrum, Chenopodium album, Echinochloa crus-galli) (Zimdahl 1980). In these circumstances the need is felt for reliable prediction of yield losses and advice for herbicide application (Cousens in prep.)

In the search for practical warning systems and thus in the development of empirical models (Spitters et al. 1983), the following characters (parameters) are put forward as useful descriptors of weed infestation:

- the time of emergence of the weed with respect to the crop emergence date (Cousens 1985, Lapointe 1985, O'donovan et al. 1985, Spitters et al. 1983),
- the weed species (provided that we have data on specific biological and physiological characters such as growth form, height and other morphological responses to competition, a.o.),
- the weed density. This parameter on its own has only a limited value, as demonstrated in many experiments on damage thresholds: large differences in yield loss - weed density relations between experiments are often found (Koch 1974, Kropff et al 1984, Poole et al. 1987, Schweizer 1981, Wahmhoff et al. 1985, Zimdahl 1980).

Plant responses to environmental factors can be quantified. For many crop species these relations are used in growth models, but data on physiological characteristics of weeds are still lacking. Present versions of the crop-weed competition models, equally based on physiological growth parameters, suggest a predominant influence of differences in the times of emergence of crop and weed, and of two biological characters, the leaf area development and plant height (Kropff et al. in prep.). However, there appear to be few complete sets of field data on growth and performance of both weed and crop in monocultures and mixtures, in well monitored environmental conditions, in different years and with different time lag between crop and weed emergence. This labourious type of field experiment is rewarding, since, apart from datasets for validation of simulation models and the testing of

hypotheses generated with the models, it offers a discriminating view on competition-related processes in the course of a growing season.

In this contribution we present the analysis of two field experiments in subsequent years, in order to evaluate the influence of the relative time of emergence, and of plant height and leaf area development, given the crop and weed species and their responses to different weather conditions.

#### EXPERIMENTAL DESIGN

The field experiments, in split plot design with four replicates, were carried out in Wageningen on a loamy sand (4% soil organic matter) with adequate supply of water and nutrients.

In 1985 sugar beet was grown at 30 cm equidistant spacing (11 plants per  $m^2$ ); the weeds were grown equally distributed between the crop plants, Fat hen at 5.5 plants per  $m^2$  in mixture and 11 plants per  $m^2$  in monoculture, Chickweed at 11 (clumps of) plants per  $m^2$ , both in mixture and monoculture. The plot size was 6 x 1.5 m, allowing harvest of 15 plants. The dates of 50% emergence for sugar beet, Fat hen and Chickweed were 9 May, 21 May and 20 May, respectively.

In 1986 sugar beet was grown in rows 50 cm apart, at distances of 18 cm in the row (11 plants per  $m^2$ ); Fat hen was equally grown in rows at plant distances of 18 cm in monoculture or in the rows of the crop, alternating with the sugar beet plants. Plot size was 6 x 1.25 m. Fat hen was sown at crop emergence and 15 days later and had final densities of 11 plants per  $m^2$  in monoculture, but in the mixtures of 9.1 and 9.7 plants per  $m^2$ , respectively. The dates of 50% emergence for sugar beet, Fat hen (early) and Fat hen (late) were 4 May, 25 May and 3 June, respectively.

#### RESULTS

The 1985 experiment produced growth curves of the type expected for the monocultures of Beta, Chenopodium and Stellaria (Fig. 1A) and illustrates the shorter life cycles of the weeds, especially Stellaria. The time lag between sugar beet and weed emergence of about 10 days leads to substantial crop losses at final harvest, but even at the beginning of July there is an influence of Beta (by then over 2 t ha<sup>-1</sup>) on the weed, especially Stellaria, and vice versa. Table 1 shows that total crop biomass was reduced with 21% by Stellaria and with 37% by Chenopodium. The time course of the height development and the leaf area index of Beta-weedfree (B), Beta with Chenopodium (Bc) and B. with Stellaria (Bs) is summarized in Table 2, as well as height and LAI for Chenopodium and Stellaria monocultures (Chm and Stm) and their mixtures with Beta (Chb and Stb). Marked differences were the height development of Chenopodium (more than twice as high as the crop) and the much higher LAI of Stellaria (LAI 2.68, against 0.96 in Chenopodium).

The 1986 experiment offers comparable results, with respect to monocultures of Beta and Chenopodium 1 (early). Apparently weather conditions (August and September being drier, colder and more clouded than 1985) were less favourable for Beta and its final production stayed well behind 1985. The weather did not affect final biomass of Chenopodium 1, emerging on May 25 (four days later than previous year), due to its shorter life cycle. Even the Chenopodium 2 (late) emerging on June 3, produced almost the same final biomass, well over 13 t ha<sup>-1</sup>.

In the mixtures only the early Chenopodium with a time lag of 21 days,

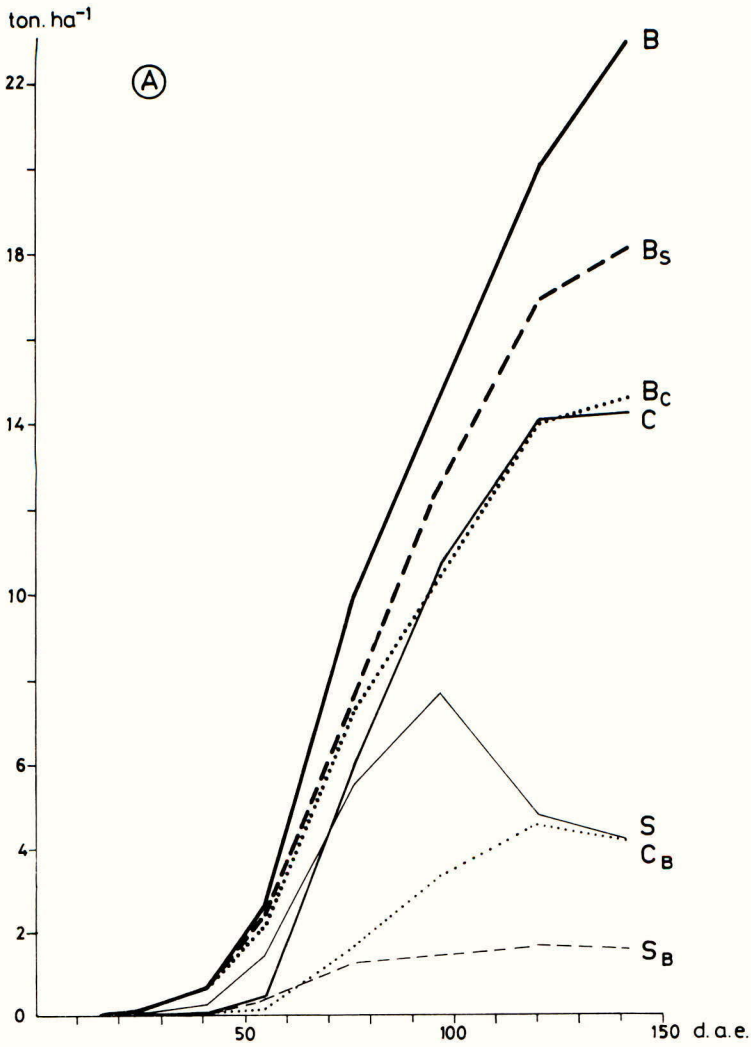


Fig. 1.A. Development of dry weight (t. ha<sup>-1</sup>) in 1985 of Beta in monoculture (B), in mixture with Stellaria (B<sub>S</sub>) and with Chenopodium (B<sub>C</sub>). Dry weight of the weeds comprise Stellaria in monoculture (S), in Sugar beet (S<sub>B</sub>) and Chenopodium in monoculture (C) and in Sugar beet (C<sub>B</sub>); dae: days after emergence of the sugar beet crop.

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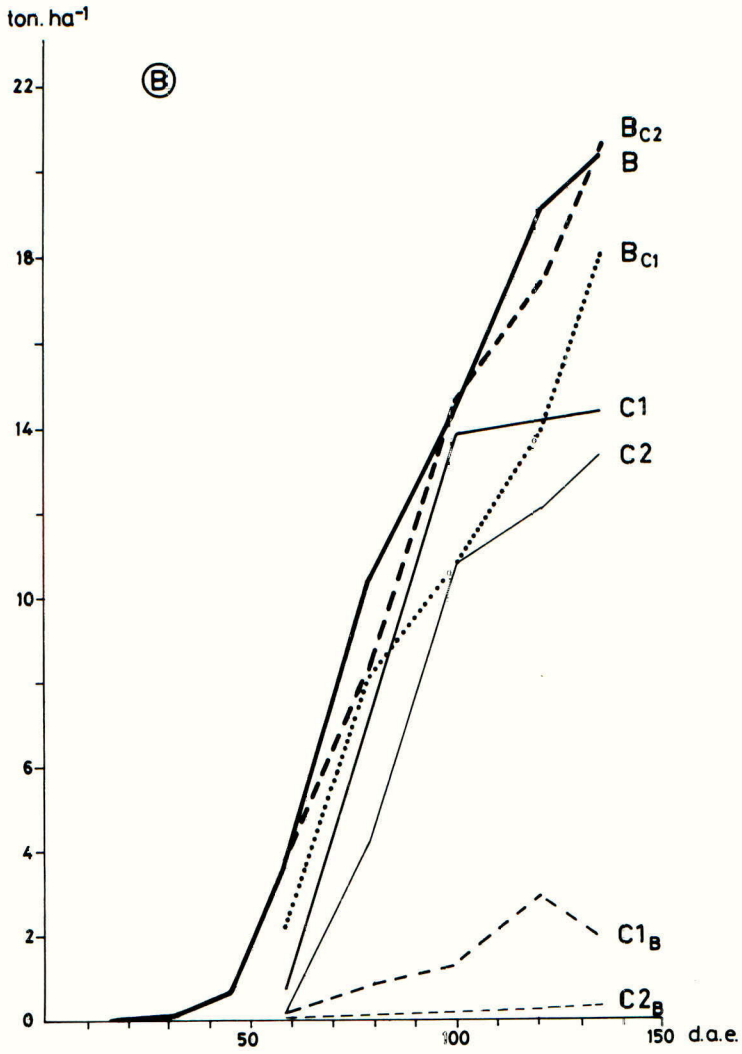


Fig. 1.B. Development of dry weight in 1986 of Beta and Chenopodium (early: C1, and late: C2) in monocultures and mixtures. (Explanation of symbols 1A).



TABLE 2

Height development in Beta (B: mono, B<sub>C</sub>: with Chenopodium, B<sub>S</sub>: with Stellaria), Chenopodium (C: mono, C<sub>B</sub>: with Beta) and Stellaria (S: mono, S<sub>B</sub>: with Beta), and development of leaf area index LAI in 1985. For 1986 height and LAI data relate to Beta and Chenopodium only, the latter sown early (C1) and late (C2). Dae: days after emergence of the crop.

Height cm (1985)								LAI (1985)						
dae	B	B <sub>C</sub>	B <sub>S</sub>	C	C <sub>B</sub>	S	S <sub>B</sub>	B	B <sub>C</sub>	B <sub>S</sub>	C	C <sub>B</sub>	S	S <sub>B</sub>
39	18	17	17	13	13	10	9	.77	.79	.85	.09	.04	.54	.21
53	34	33	32	53	53	21	22	2.35	1.98	1.94	.81	.24	3.30	1.15
74	50	51	51	142	127	35	50	5.65	3.97	4.03	4.63	.96	10.61	2.68
95	62	57	60	159	145	29	56	5.10	4.17	3.87	4.73	.80	9.33	2.68
118	59	58	60	166	142	-	-	5.10	4.19	4.13	4.24	.59	1.26	.67
140	61	59	56	159	142	11	53	4.66	3.27	3.08	1.15	.12	.58	.17

Height cm (1986)*						LAI (1986)						
dae C1	dae C2	C1	C1 <sub>B</sub>	C2	C2 <sub>B</sub>	B	B <sub>C1</sub>	B <sub>C2</sub>	C1	C1 <sub>B</sub>	C2	C2 <sub>B</sub>
28	38	28	28	12	13	2.29	2.22	2.56	.81a	.18b	.23b	.02c
48	58	136	72	101	31	3.36	2.73	2.40	3.43a	.27a	2.98b	.07c
69	79	158	74	158	43	3.77	2.89	3.34	3.75a	.29a	3.78b	.07c
90	100	159	92	156	43	3.18	2.50	3.15	3.33a	.26a	3.78b	.05c
104	114	156	81	149	45	2.85	2.79	3.11	2.64a	.05a	2.67b	.03c

\* Height of Beta compare data 1985

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reduced Beta production with 11% at final harvest (Table 1B); already on July 1st a lowering of Beta biomass and of Chenopodium biomass is shown (Fig. 2).

TABLE 1

The 1985 and 1986 sugar beet production at final harvest in mono- and mixed cultures, in  $t, ha^{-1}$  and in (%) of weed-free.

Different letters indicate significant difference between treatments ( $P < 0.05$ , capitals  $P < 0.01$ ).

1985		weed-free	with Stellaria	with Chenopodium
Total dry weight	( $t ha^{-1}$ )	23.1 (100) a(A)	18.2 (79) b(AB)	14.6 (63) b(B)
Shoot dry weight	( $t ha^{-1}$ )	8.6 (100) a(A)	6.8 (80) b(AB)	6.4 (74) b(B)
Root dry weight	( $t ha^{-1}$ )	14.5 (100) a	11.3 (78) ab	8.2 (57) b
Total fresh weight	( $t ha^{-1}$ )	61.9 (100) A	48.9 (79) B	33.1 (53) C
Sugar content (%)		15.04 a	15.43 b	15.43 b
Sugar production	( $t ha^{-1}$ )	9.3 (100) A	7.5 (81) B	5.1 (55) C

1986		weed-free	with early Chenopodium	with late Chenopodium
Total dry weight	( $t ha^{-1}$ )	20.3 a	18.1 b	20.5 a
Shoot dry weight	( $t ha^{-1}$ )	7.4 -	6.9 -	7.0 -
Root dry weight	( $t ha^{-1}$ )	12.9 a	11.2 b	13.5 a
Total fresh weight	( $t ha^{-1}$ )	53.5 a	45.4 b	56.3 a
Sugar content (%)		17.7 -	17.9 -	18.0 -
Sugar production	( $t ha^{-1}$ )	8.5 a	7.3 b	9.0 a

### CONCLUSIONS

#### LAI and height

The results of the 1985 experiment show marked differences between the two weed species, Chenopodium causing by far the highest yield loss. Supply of water and nutrients taken as sufficient, the competition will have been for light exclusively. This result stands in marked contrast to the lower yield loss by Stellaria, which had a strong leaf area development (LAI 2.7 and in its monoculture even 10) compared to Chenopodium (LAI 0.96 and in monoculture 4.6). This is explained by the data on height development (Table 2). In monoculture Chenopodium plants grew up to a height of 160 cm and up to 150 cm between the sugar beets, which topped at 60 cm, and was able to use its lower LAI more effectively in the light interception. Stellaria in monoculture remained of low stature (35 cm), but part of it used the beet plants to climb up to the same height as the crop.

### Relative time of emergence

The results of the 1986 experiment clearly show the strong effect of a difference of 10 days in the period between sugar beet and weed emergence. The latest sown weed did not gain a high stature, reached only modest LAI and finished its growth together with the early sown weed, at the end of a shorter life span and without seriously hampering crop production.

### DISCUSSION

Height- and leaf area development, together with emergence date and two differing years, they once more revealed their serious influence on the outcome of crop-weed competition (viz. also Elberse et al. 1979, Lapointe 1985).

On the one hand the relative date of emergence proves to be an indispensable datum in any discussion of competition and it is amazing that in many publications this aspect is neglected.

The results draw attention to the germination and to developmental characteristics of the weeds and above all to the rate of leaf area development and height growth of the weeds relative to the crop canopy. Although Chenopodium is known for its capacity to increase height in a shadowy environment, the plants of the later generation in the 1986 experiment did not develop a canopy on top of the crop's. Shortening daylength urged the onset of flowering and although the weed had a substantial production including a seed crop, it did not interfere with the sugar beet.

The results of the present experiments, although permitting clear conclusions, cannot lead to causal understanding or generalization. This is only to be expected from simulation studies based upon knowledge of the underlying physiological processes, governing photosynthesis and morphological development (height growth, lateral spread, leaf development). The hypotheses generated may lead to relatively simple and less casuistic field experiments.

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