

## BOTANICAL BRIEFING

# The Theory and Application of Plant Competition Models: an Agronomic Perspective

SARAH E. PARK<sup>1,\*</sup>, LAURENCE R. BENJAMIN<sup>2</sup> and ANDREW R. WATKINSON<sup>3,4</sup>

<sup>1</sup>*School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK*, <sup>2</sup>*Rothamsted Research, Harpenden, Hertfordshire, UK*, <sup>3</sup>*Schools of Biological and Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK* and <sup>4</sup>*Tyndall Centre for Climate Change Research, University of East Anglia, Norwich NR4 7TJ, UK*

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Many studies of plant competition have been directed towards understanding how plants respond to density in monocultures and how the presence of weeds affects yield in crops. In this Botanical Briefing, the development and current understanding of plant competition is reviewed, with particular emphasis being placed on the theory of plant competition and the development and application of mathematical models to crop–weed competition and the dynamics of weeds in crops. By consolidating the results of past research in this manner, it is hoped to offer a context in which researchers can consider the potential directions for future research in competition studies and its application to integrated weed management.

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**Key words:** Competition, weed management, modelling, crop–weed interaction, experimental design.

## INTRODUCTION

The decline in weed seed numbers in arable fields (approx. 95%) over the course of the 20th century is witness to the success of weed control measures (Robinson and Sutherland, 2002). This success in weed control has resulted primarily from the extensive use of herbicides, changes in crop rotations and a range of cultivation methods. However, the sustained use of a range of agro-chemicals, in recent years, has resulted in an increase in the number of herbicide-resistant weed species (Powles and Shaner, 2001), a shift in the weed flora of arable fields from one of mixed weeds to one dominated by grass weeds (Barr *et al.*, 1993) and increasing environmental and public health concerns over the use of pesticides (Conway and Pretty, 1991).

As a consequence, there is an increasing interest in methods of weed control that allow a reduction in the use of herbicides. This is reflected in the increased interest in non-chemical methods of weed control (Weiner *et al.*, 2001), organic farming (Lampkin, 2003) and the use of intercropping (Vandermeer, 1989). Recently, it has also been argued (Dewar *et al.*, 2003) that the use of genetically modified herbicide-tolerant crops with glyphosate and glufosinate herbicides may allow a more flexible, knowledge-based management to weed control, permitting higher weed populations early in the season than is possible in conventional systems to promote biodiversity. If such systems are to be employed, however, it is essential that the impact of delayed control on the competitive balance between weeds and crop is fully understood, if yields are not to be reduced.

\* For correspondence. Present address: CSIRO, Sustainable Ecosystems, Level 3, Queensland Biosciences Precinct, St Lucia, QLD 4067, Australia. E-mail sarah.park@csiro.au

Clearly, the efficacy of using agronomic practices to manage weed populations will be improved by a comprehensive understanding of the mechanisms of competition. Mathematical models to describe the process of plant competition have developed concurrently with our increasing empirical understanding. The structure of models has reflected the prevailing approach to weed management. Earlier research was focused on the calculation of yield loss as a result of weed competition and an empirical modelling approach. A more recent interest in managing competition, through increased knowledge of the ecology and biology of competing species, has resulted in an increase in the use and development of more mechanistic-based and dynamic population models for weeds. Used as either a tool for research or as a method for prediction, the mathematical model is an essential and integral part of the study of plant competition.

The aim of this Botanical Briefing is, first, to provide an overview of our current understanding of the mechanisms of competition at the individual plant level and, secondly, to review the development of mathematical models of plant competition, particularly in their application to the management of agricultural weeds. It is the aim to provide an overview of the broad spectrum of approaches that have been adopted within the study of plant competition as it relates to weed management. The focus here is on the quantification of intraspecific and interspecific competition in the crop–weed environment, and on the impact of competition on plant performance within the growing crop and weed population dynamics. By consolidating the results of past research in this manner, it is hoped to offer a context in which researchers can consider the potential directions for future research in competition studies and its application to weed management.

## THEORIES OF COMPETITION

Whilst definitions of competition abound, they can typically be divided into two categories, those that focus on mechanisms and resource acquisition (e.g. Tilman, 1982; Grime, 2001) and those that focus on the reduction in fitness brought about by a shared requirement for a resource in limited supply (Silvertown and Charlesworth, 2001). In crop–weed competition studies, it is the mechanistic modelling approach that highlights the importance of the acquisition and pre-emption of resources in the competitive process. In contrast, it is the definitions of competition that focus on fitness that have influenced the development of phenomenological models of crop–weed competition and the quantification of yield loss and the dynamics of weeds in agro-ecosystems.

## INTRASPECIFIC COMPETITION

Much of the present understanding of intraspecific competition in plant populations is credited to a series of papers written in the 1950s and 60s by a group of Japanese researchers (Yoda *et al.*, 1963). In summary, the papers identified three principal effects resulting from intraspecific competition in monocultures: a competition–density effect (decrease in mean size of surviving plants with increasing density); alteration in the size structure of the population (size hierarchy development); and density-dependent mortality (self-thinning). The process of self-thinning is not described here (see Yoda *et al.*, 1963) as plants in an agronomic environment rarely reach the combinations of weights and densities where self-thinning would be expected to occur (Enquist *et al.*, 1998).

*Competition–density effect*

The early pioneering studies on plant monocultures stimulated considerable interest in the mathematical description of the relationship between plant performance and density. The decline in plant performance with density as a result of competition was found to be best described by a reciprocal equation (Shinozaki and Kira, 1956; Bleasdale and Nelder, 1960; Watkinson, 1980) of the form

$$w = w_m(1 + aN)^{-b} \quad (1)$$

where  $w$  is mean plant weight,  $N$  is plant density,  $w_m$  is the mean dry weight of an isolated plant at a given time, and  $a$  and  $b$  are parameters (Watkinson, 1980). Parameter  $a$  is related to the density at which intraspecific competition has an impact on yield and parameter  $b$  determines whether the yield–density relationship is over-turning ( $b > 1$ ), asymptotic ( $b = 1$ ) or monotonically increasing ( $b < 1$ ) with density. The parameters  $w_m$  and  $a$  are typically positively correlated (Watkinson, 1984; Li *et al.*, 1996) as parameter  $a$  can be considered as the area of resources required to produce a yield of  $w_m$  in an isolated plant. This model or similar has been successfully used to describe yield–density relationships in a wide range of plant monocultures and lies at the heart of describing density-dependent processes that result from competition in plant populations.

*Alteration in the size structure of the population*

Quantifying the size structure of a population is clearly an important pre-requisite for determining the role of plant competition; the most often used measurements are the shape of histograms (skewness), the coefficient of variation and the Gini coefficient (Weiner and Solbrig, 1984). Koyama and Kira (1956) made the first studies of changes in the frequency distribution of biomass in plant monocultures with time and density. They presented evidence that frequency distributions of herbaceous and tree species were symmetrical during the early stages of growth, with the distribution shifting progressively towards a positive skew with time. They pointed out that this could be explained as the inevitable consequence of exponential growth and a symmetrical distribution of relative growth rates. Hence, the development of log-normal weight frequency distributions is not proof of competitive interactions between plants.

There is, however, evidence that competition plays a major role in generating the plant-to-plant variability in relative growth rates that affect frequency distributions of weight (Weiner and Thomas, 1986) and that the symmetry of competition also affects the development of frequency distributions. Asymmetrical competition occurs when a small number of large individuals utilize a disproportionately large share of the available resources to the detriment of the growth of smaller neighbours. In symmetrical competition the growth of each plant is in proportion to its size. In general, asymmetrical competition leads to greater inequality of biomass within a population. There are, however, complex interactions between the spatial arrangement of plants, the nature of the resource, the spatial heterogeneity of the resource, the episodic availability of the resource and the plant's physiological and morphology response to levels of resource supply (Schwinning and Weiner, 1998). Because of these complex interactions, it is not possible to conclude that the development of inequality of size is proof of asymmetrical competition.

The development of a size hierarchy has been described by numerous population models (e.g. Westoby, 1982; Firbank and Watkinson, 1985a; Benjamin, 1988; Pacala and Weiner, 1991), and many factors, such as the number of neighbours and relative emergence time, have been considered as important in determining the position of an individual within a size hierarchy (Benjamin and Hardwick, 1986; Wyszomirski *et al.*, 1999). However, despite the obvious commercial importance of variability in plant size, especially in vegetable crops that need to meet strict size limits to be marketable, models of the development of size hierarchies have not been exploited to this end. Models to predict the effect of agronomic practices on changes in size structure of populations have instead relied upon estimating changes in the parameter values of frequency distribution curves from empirically derived relationships (Benjamin *et al.*, 1999).

## INTERSPECIFIC COMPETITION

Agronomic studies aimed at quantifying competition between two species most commonly consider a weed and

crop species and, to a considerably lesser extent, two crops grown in an intercrop. A variety of experimental designs and statistical analyses have been used to study competition in mixtures (Gibson *et al.*, 1999; Freckleton and Watkinson, 2000). Here the focus is on the replacement series, and additive and neighbourhood designs.

#### Replacement series

The replacement series approach involves growing two species in varying proportions, including monoculture, whilst maintaining a constant overall stand density (de Wit, 1960). Considered as pioneering in the analysis of competition within mixtures, it has also attracted much criticism, particularly regarding the dependence of the model coefficients on total stand density (Inouye and Schaffer, 1981; Connolly, 1986) and the inability of the model to dissociate the separate effects of intra- and interspecific competition (Firbank and Watkinson, 1985b; Snaydon, 1991) especially under changing conditions (Watkinson and Freckleton, 1997). Notwithstanding these shortcomings, the replacement series still has adherents, albeit conditional. We would, however, argue that it is an inappropriate design for the analysis of competition in agronomic environments where understanding of how the effects of competition vary with density is of key concern (see below).

#### Additive design

Additive designs refer to those experiments where both the density and proportion of species are varied in mixtures. In its simplest and most typically applied form in an agricultural context, the so-called 'partial additive design' allows the density of one species to be held constant whilst the second species is varied over a range of densities. Consequently, this design is particularly favoured for the study of crop–weed competition, although the data generated by this design can provide only a limited picture of the interaction between species, because it provides no information on the effect of the crop on the weed. One formulation of the hyperbolic model that has been used commonly for describing the damage to crop yield caused by competition from weeds (Cousens, 1985) is

$$Y_L = iN_w(1 + ia^{-1}N_w)^{-1} \quad (2)$$

where  $Y_L$  is the proportion of yield lost,  $N_w$  is weed density,  $i$  is the percentage yield loss per weed plant at low weed densities and  $a$  is the upper limit to yield loss at high weed densities. This equation may be further modified to take account of differences in competition between the weed and crop that result from differences in emergence time (Cousens *et al.*, 1987)

$$Y_L = bN_w(e^{cT} + ba^{-1}N_w)^{-1} \quad (3)$$

where  $T$  is the time in days between emergence of the crop and the weed and  $a$ ,  $b$  and  $c$  are parameters. Kropff and Spitters (1992) took an alternative approach for accounting

for differences in emergence times by weighting densities with the average leaf area index.

The popularity of the hyperbolic model is in part due to its ability to satisfy what Cousens (1985) reasons to be the four fundamental biological truths of crop–weed competition: (1) there will be no yield loss in the absence of weeds; (2) the effects of increasing weed numbers will be additive at low weed densities; (3) crop yield loss can never exceed 100%; and (4) there is a non-linear response of crop yield to weed density at high weed densities. The model is sometimes criticized because it offers little explanation of the underlying processes determining the outcome of competition and because there are difficulties in extrapolating to a broad range of species or locations. The model is, however, readily parameterized and with data taken from a range of sites at different times, it is possible to generalize about the factors playing the greatest role in determining yield loss.

While the partial additive design typically involves growing one species at a constant density while varying that of the other, an extreme version involves growing a species with and without interspecific competition. This has led to the development of a range of indices to quantify competition by essentially comparing the performance of a plant in monoculture with that in a mixture. Despite some endorsement of the use of such simple composite indices in conjunction with this experimental design (Cousens, 1991; Snaydon, 1991), they allow only a crude picture of the competitive process to emerge. Once again, the indices are sensitive to density and may erroneously attribute the effects of a change in environmental conditions on relative performance in mixtures to changes in interspecific competition (Freckleton and Watkinson, 1997).

At the opposite end of the extreme, the additive series involves replication of the full complement of density combinations for two species over a wide range of densities. It allows the quantification of both intra- and interspecific competition when analysed using a two-species regression model (Pantone and Baker, 1991; Park *et al.*, 2002). More generally for this form of analysis, the single species model (eqn 1) can be extended to two or more species using the relationship

$$w_i = w_{m,i}(1 + \sum \alpha_{ij}N_j)^{-b} \quad (4)$$

where  $w$  is a measure of plant performance,  $w_m$  is the performance of an isolated plant and  $\alpha$  represents the per capita effects of intra- ( $\alpha_{ii}$ ) and interspecific ( $\alpha_{ij}$ ) competition (Watkinson, 1985).

#### Neighbourhood design

The neighbourhood approach to analysing plant competition was pioneered by Mack and Harper (1977) and involves relating the performance of an individual target species to the density of a neighbouring species within a given proximity. This design is based on the assumption that the performance of a target plant is related to the number, biomass, cover, aggregation or distance of the neighbouring species. However, the data requirements for neighbourhood models may be particularly resource-intensive and can yield

similar results to less spatially explicit mean density models (Pacala and Silander, 1990). Nevertheless they are of particular value where competition needs to be quantified under different spatial arrangements of plants, although they have been used little within this context in agricultural studies.

#### *Experimental design and analysis*

Whilst the debate regarding the most appropriate experimental design and method of quantifying competitive intensity in mixed species stands continues to attract a lively discussion (Freckleton and Watkinson, 1999; Jolliffe, 2000; Connolly *et al.*, 2001), there is an increasing consensus that the range of inferences that may validly be drawn from a study are principally determined by the experimental design used (Gibson *et al.*, 1999; Freckleton and Watkinson, 2000). There is, however, no optimum design for competition experiments since the aims, objectives and practicalities vary from study to study and species to species. However, the fact that an overwhelming number of studies have shown that the effects on performance of competition in plant mixtures may be described by simple hyperbolic models, indicates that the problem of measuring plant competition is one of regression (Freckleton and Watkinson, 2000). Moreover, theory has shown that, of the available methods, the regression approach is generally the most robust for analysing competition under field conditions (Freckleton and Watkinson, 2001a). This argues for comparable approaches to the study of plant competition under both controlled environment and field conditions if we are to understand better how changing conditions and resources affect the process of competition in the agricultural environment and the consequent impacts of competition on crop yield and weed performance.

### DYNAMIC MODELS OF PLANT GROWTH AND COMPETITION

Models of plant competition are predominantly categorized as being either phenomenological, providing only a description of the outcome of competition, or mechanistic in structure, offering a representation of the physiological processes underlying plant growth. Competition studies that consider only final yield are inevitably limited as to the inferences that may be drawn about the process of competition. Quantitative measures of growth taken during the course of a growing period are necessary to understand the changing dynamics of species interactions and elucidate the competitive mechanisms determining the growth of individuals over time. Further, dynamic growth analysis allows the dissociation of ontogeny, the phenotypic developmental trajectory of an individual, from environmental effects on growth (Evans, 1972).

Mechanistic models and, in particular, eco-physiological models based on the response of physiological processes in plants to their environment, generally contain many parameters. As parameter estimates may be difficult to derive and consequently contain substantial error, the use of mechanistic models as a tool for decision-making is

regularly found to be impractical. However, the development of more parsimonious mechanistic plant growth models has resulted in a general increase in their use in recent years (Graf and Hill, 1992; Kropff and Spitters, 1992; Aikman and Scaife, 1993; Deen *et al.*, 2003).

The capture of resources, particularly the interception of solar radiation, is an important factor in determining the competitive ability of species and this is reflected in light interception being the most developed aspect of many eco-physiological models. For example, Spitters and Aerts (1983) proposed a model that was further developed by Kropff and colleagues (Kropff, 1988; Lotz *et al.*, 1990; Kropff and Spitters, 1992), which took account of the spatial position of leaves and roots by dividing the canopy and root zone into a number of horizontal strata. Simulated growth was then partitioned between two species according to their relative proportional contribution to total leaf area. A less detailed approach to simulating growth within a multi-species canopy was taken by Ryel *et al.* (1990), who estimated the photosynthetic potential of foliage positioned in sunlit and shaded areas of the canopy. Rimmington (1984) provided a simpler model in which competition for light was simulated by dividing the canopy into only a small number of strata.

The above models all differ in the amount of detail expended on quantifying the local availability and interception of light. Interestingly, Deutschman *et al.* (1999) demonstrated that the amount of detail used to describe the local availability of light using the mechanistic, spatially explicit, stochastic forest simulation model, SORTIE (Pacala *et al.*, 1996), had surprisingly little effect on the accuracy of its predictions at the forest development level. Nonetheless, a less detailed quantification of light does alter the predicted growth and mortality rates at the level of the individual tree.

Eco-physiological models have been developed to include resources, such as nitrogen (Graf *et al.*, 1990; Wilkerson *et al.*, 1990), in addition to light while the Conductance Model (Aikman and Scaife, 1993) offers a simple mechanistic approach to simulating the growth of similar and different height species in monoculture and mixtures as a function of multiple resources (Park *et al.*, 2001). Cellular automata models have also been used to describe the development of an individual in response to a heterogeneous resource supply (Colasanti and Hunt, 1997).

Dynamic models of plant growth and competition, however, have had little impact to date on the design of weed management programmes. Despite the obvious potential application of such models to crop–weed competition through, for example, the manipulation of the canopy of the crop to suppress weeds (Weiner *et al.*, 2001) and the delay in herbicide spraying to allow weed growth during the early stages of crop development to promote biodiversity (Dewar *et al.*, 2003). The problem lies in the intensive studies required for successful parameterization.

#### *Population dynamics*

To understand the population dynamics of a species through time requires understanding of the various density-

independent and density-dependent processes that affect the numbers of births and deaths in a population. Population models are based on censuses of plants at either flowering or germination and predict population size of species  $i$  ( $N_i$ ) at time  $t + 1$  as a function of the population sizes at time  $t$  using a hyperbolic equation of the form

$$N_i(t + 1) = \lambda_i N_i(t) (1 + \sum \alpha_{ij} N_j)^{-b} \quad (5)$$

The parameters of eqn (5) are the finite rate of increase,  $\lambda$ , defined as the maximal mean rate of population increase from low densities and competition coefficients,  $\alpha$ , that model the *per capita* effects of intraspecific ( $\alpha_{ii}$ ) and interspecific ( $\alpha_{ij}$ ) competitors. This formulation can readily be extended to include a seed bank (Freckleton *et al.*, 2000; Watkinson *et al.*, 2000a) and allows the dynamics of the species to be modelled using parameters that can be estimated directly from data on counts of numbers of plants.

Population models of the sort described by eqn (5) have been applied to a range of weed species including *Alopecurus myosuroides* (Doyle *et al.*, 1986), *Anisantha sterilis* (Firbank *et al.*, 1985; Smith *et al.*, 1999), *Avena fatua* (Pandey and Medd, 1991; Jones and Medd, 1997), *Chenopodium album* (Freckleton and Watkinson, 1998) and *Vulpia bromoides* (Freckleton *et al.*, 2000). A critical component of all of the above models is quantification of the strength of both intra- and interspecific competition. In all cases, this was carried out through the manipulation of densities and the use of regression analysis to estimate the competition parameters in eqn (5), using either population growth rate or some measure of plant performance (e.g. seed production) as the dependent variable. Sensitivity analysis allows the understanding of key parameters of the life cycle that determine population numbers and highlights areas of the life cycle at which controls may be effective. In the case of *Chenopodium album*, this allowed Freckleton and Watkinson (1998) to conclude that predicting the effects of changing management on long-term abundance of the weed will benefit more from improved systems for understanding germination behaviour than through management of the competitive ability of the crop, which will be effective only if very large changes in competitive effect can be achieved.

#### FACTORS INFLUENCING THE OUTCOME OF COMPETITION

If the intrinsic weed-suppressing ability of a crop is to be exploited (Weiner *et al.*, 2001), it is necessary to identify the ecological and life-history traits that confer competitive ability. Numerous life-history traits have been credited as determining the competitive ability of an individual plant or species. Many of these traits are morphological (e.g. biomass partitioning) and display considerable phenotypic plasticity that can be exploited by a plant in a competitive environment. Several other traits have also been identified as potential determinants of competitive ability; these include seed size (Rees, 1995), seedling size (Schwinning and Fox, 1995), emergence time (Kropff and Spitters, 1991) and plant size (Goldberg and Landa, 1991). All of these

parameters, in one way or another, either influence or reflect the ability of an individual plant to capture resources.

Whilst life history traits *per se* offer some explanation for the competitive ability of an individual or a species, the relative difference between two competing individuals or species is increasingly being recognized as an important determinant of the outcome of competition (Freckleton and Watkinson, 2001b). The most common life history traits considered in terms of the relative difference between individual species are the relative time of emergence (Elberse and de Kruijf, 1979; Cousens *et al.*, 1987), relative leaf area (Kropff, 1988) and relative biomass (Goldberg and Landa, 1991; Freckleton and Watkinson, 2001b). In an analysis of the competitive relationships between seven species, Freckleton and Watkinson (2001b) found that competition coefficients relate strongly to differences between the maximum sizes, root allocation, emergence time and seed size of species. The best predictor, however, was the difference in the maximum size of plants grown in isolation; correlations of the other traits with the competition coefficients occur through effects on the maximum size. The analysis also revealed coefficient reciprocity (inverse relationships between the interspecific coefficients for species pairs) and transitivity (numerically predictable hierarchies of competition between species). The theoretical basis for expecting coefficients to follow these patterns relates to short-term competition for limiting resources.

It should be noted at this point that the strength of competition measured from experiments that consider plant weight as the dependent variable is not necessarily the same as the strength of competition in a population dynamic sense (Chesson and Huntly, 1997). Caution should therefore be exercised in making inferences about the outcome of competition from studies on plant performance alone. The outcome of competition in a population dynamics sense depends not only on the magnitude of the competition coefficients but also on the finite rate of population increase (Watkinson *et al.*, 2000a).

#### PRACTICAL APPLICATION OF CROP-WEED COMPETITION MODELS

Crop-weed competition models have been used extensively for determining the yield loss of crops that result from varying densities of weeds. In one of the simplest extensions of this approach, knowledge of crop-weed competition has been combined with herbicide-weed resource curves to simulate the effects of herbicide use on crop yield and provide a rudimentary economic evaluation of herbicide treatments (Streibig, 1989). A more refined economic analysis has been achieved through the use of bioeconomic models. These consist of several sub-models, typically describing the life cycle of the crop and weed, crop-weed competition and economic system (Dunan *et al.*, 1993; Jones and Medd, 1997).

In an alternative approach, crop-weed models have been applied to the task of identifying the minimum, or 'threshold', density of weeds justifying weed control. The threshold is calculated as the weed density at which the cost of chemical control is equal to the net benefit on crop yield

gained through a reduction in weed competition. Such a modelling approach is not without its critics, particularly on the grounds of insufficient data, uncertainty and the non-random distribution of weeds (Auld and Tisdell, 1987; Dent *et al.*, 1989). In a recent review, Wilkerson *et al.* (2002) argued that weed management decision models should be evaluated from the perspectives of biological accuracy, quality of recommendations and ease of use. They further argued that future use depends upon finding cost-effective methods to assess weed populations, demonstrating that the use of models makes more better decisions and that there is stable long-term funding for the maintenance and support for the models.

Whilst the primary motivation behind many threshold models has been an improvement in the cost-effectiveness of using herbicides, integrated weed management models, which simulate a combination of different chemical, mechanical, cultural, generic and biological weed control methods, provide a more sustainable approach to weed control. By using a selection of sub-models to describe biological processes, including crop–weed competition, decision aids such as WEEDSIM (Swinton and King, 1994) and WEEDCAM (Lybecker *et al.*, 1991) simulate the long-term outcome of a mix of different management options on the environment, given an initial estimate of the weed seed bank or seedling population. Despite offering a potentially valuable tool for assessing the environmental, as well as the economic costs of weed management strategies, the use of mathematical models in integrated crop protection has, to date, been markedly under-utilized.

The quantification of competition together with the finite rate of population increase is at the heart of these models. Examples of their range of application include explanation of the decline in a previously common weed (Firbank and Watkinson, 1986), predicting strategies that provide economic control of weeds (Cousens *et al.*, 1986; Doyle *et al.*, 1986; Watkinson *et al.*, 2000a), contrasting the impacts of broad-scale changes in farm management for the dynamics of weeds (Smith *et al.*, 1999) and predicting the potential impacts of new technology on the species that feed on weed seeds (Watkinson *et al.*, 2000b). Weed population models are thus being used to address a range of questions that would be impossible to tackle without quantification of plant competition. It is for this reason that the experimental designs and analyses that are used to quantify competition are of such importance.

## CONCLUSION

Crop–weed models incorporating competition have had considerable success in describing how the process of competition affects crop yield and how strategic weed management decisions impact on weed numbers for a limited range of economically important species. There is, however, a need to increase our understanding of the spatial and temporal variability in model parameters if they are to be used more in a predictive context and to pull together data for a wide range of weeds and crops.

In contrast, mechanistic models have to date had limited success in describing crop–weed competition and limited

utility within the weed management process. The problem with such models is that they require very intensive studies to be successfully parameterized and are constrained by their inherent need for detailed information relating to key physiological processes. For this reason, the development of more parsimonious models would be an advantage, requiring a more general approach to the study of competitive and physiological processes, enabling insight beyond that of the individual species.

Exploration of integrated weed management requires that we understand how weed management decisions within the crop growing-season affect: (a) the yield of the crop through competition for resources, and (b) the biodiversity and numbers of weeds in the current and future crops. Both mechanistic and phenomenological models have a role to play here. The former include sufficient detail of the relationships between plant traits and the environment to allow exploration of within-season management decisions on crop yield, while the latter, although not including such intricate detail, allow exploration of strategic management decisions on the abundance of weeds through the crop rotation.

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