LITERATURE REVIEW

WEED CENTRED MANAGEMENT

Historically there has been a gap between weed management and weed biology/demographics. Weed management traditionally has concerned itself only with immediate crop yield with short-term economics being the primary consideration. Zimdahl (1980) has cited more than 550 papers that describe the outcome of various weed-crop interactions, the majority of which have focused only on the immediate yield losses. By focusing on the outcome of weed-crop interference many weed scientists have failed to adequately describe the mechanisms of this interference (Weldon and Slausen, 1986).

This crop-centred approach was acceptable when mechanical and chemical inputs were relatively inexpensive and considered to have only limited environmental and health effects. However, increasing necessity to reduce input costs, increasing environmental safety concerns, and increasing weed resistance to herbicides, are all putting greater pressure on producers to reduce herbicide use and to consider the long-term impact of their weed management decisions. Evaluation of weed management systems under this weed-centred approach requires more sophisticated techniques and analysis than does the traditional crop-centred approach. Adoption of these more sophisticated techniques and analysis will provide weed scientists with a more thorough quantitative insight into weed biology/demographics and their
effects on crop yield. Such insights will lead to more effective and integrated weed management systems and encourage the use of alternate non-chemical methods of weed suppression.

**PLANT CHARACTERIZATION**

**Characteristics of the Ideal Weed**

Many researchers have tried to describe the typical characteristics of plants that assure their survival and competitiveness. These descriptions range from the evolutionary strategies described by Pianka (1970), the life history theories of Grime (1977) to the competitive trait lists of Baker (1974) and Patterson (1982).

The relationship of a plant to its environment can be described on the basis of its evolutionary specialization. One approach of this type is the widely used concept of r- and K-selection (Holt, 1988). In relation to another organism an r-selected organism is one which is better adapted to survival in unpredictable environments whereas a K-selected organism is relatively better adapted to survival in a stable environment. Weeds and crops generally tend to be r-selected organisms (Radoevich and Holt, 1984).

Grime (1977) proposed that plants can be characterized by the degrees of stress and disturbance to which they were adapted. In his triangular system plants adapted to low levels of stress and disturbance are termed competitive, those adapted to high stress and low disturbance are termed stress-tolerant, and those adapted to low stress and high disturbance are termed ruderals. The ruderal and stress tolerant strategies correspond to r- and K-selection, respectively. Competition is an alternative strategy devised by Grime. Grime has
stated that competition is largely a reflection of a plants ability to capture resources and that relative growth rate is one of the best indicators of a plants competitive ability.

Weeds have characteristicly similar traits which have been compiled in various lists by different researchers (Baker, 1974; Bazzaz, 1979; Patterson, 1982 ). These lists often include several of the following characteristics which can generally, but not exclusively, be classified as either "longevity (survival) aids or interference aids:

Longevity (Survival) Aids

1. Physiological and/or morphological crop mimicry
2. Vigorous, easily fragmentable vegetative reproduction
3. Copious and continuous seed production
4. Seed production in a wide range of environments
5. Short and long distance dispersal of reproductive components
6. Self-compatible with some outcrossing by general vectors
7. Internally controlled dormancy and longevity of seed
8. Non-specific germination requirements

Interference Aids

1. Effective physical or chemical interspecific interference mechanisms (e.g. smothering growth, climbing habit, allelopathy)
2. Phenotypic plasticity
3. Photosynthetic efficiency (C4 vs. C3)
4. High water use efficiency
5. High initial relative growth rate and rapid growth
The weed traits listed above are considered, by the researchers who compiled these lists, to be the major characteristics important for weed success. Many of these traits can be quantified and are characteristic of specific weeds in populations and in isolation.

Knowledge of how weeds grow is a fundamental requirement of understanding the many characteristics of weeds that are responsible for their survival and interference. Applying the techniques of growth analysis is one way to obtain this fundamental knowledge.

**Growth Analysis**

Over the years researchers have developed indices to summarize or facilitate interpretation of primary measurements of plants or plant components. The calculation of such indices is referred to as growth analysis. Because growth analysis simply restates primary measurements in some new form it is considered a deductive rather than a predictive process.

The term growth analysis encompasses all approaches used to measure and interpret physiological, developmental, environmental and genetic sources of yield variation. The particular approach used is dependent on the goal of the analysis and falls into three main categories: conventional plant growth analysis, yield component analysis, and sub-organismal demographic analysis (Jolliffe - personal communication).

**Conventional Growth Analysis.**

Conventional growth analysis began in 1919 with the discussions of Blackman on what
is now termed relative growth rate (Hunt, 1978a). This method assumes that growth and yield are a function of contributing primary elements. This approach is time based and therefore requires primary observations to be made more than once over the growing season.

Conventional growth analysis has evolved into two main sub-approaches, the classical and the functional. The classical approach is characterized by a large number of plants being sampled at relatively infrequent harvests whereas the functional approach is characterized by frequent harvests where relatively few plants are sampled. The functional approach, first introduced by Vernon and Allison (1963), is now generally considered to be the superior approach (Radford, 1967; Hunt, 1979). The main debate associated with the functional approach is the appropriateness of various functions for fitting the data (Hurd, 1977; Venus and Causton, 1979; Meek et al., 1991).

**Conventional Analysis Growth Indices.** Conventional plant growth analysis embraces a large number of indices for interpreting plant growth. It can be classified into five major categories: indices of plant persistence (Leaf Area Duration, LAD; Biomass Duration, BMD); indices of plant presence (Species Population Density, D; Species Biomass Density, B_D); indices of rates and efficiencies of growth (Absolute Growth Rate, AGR; Relative Growth Rate, R; Crop Growth Rate, CGR); indices of the extent of the assimilatory system (Leaf Area Ratio, LAR; Specific Leaf Area, SLA; Leaf Weight Ratio, LWR; Leaf Area Index, LAI); and an index of dry matter partitioning (Harvest Index, H) (Jolliffe - personal communication). Further details on the various classical growth analysis indices and their
functions can be found in the references and reviews of Causton and Venus (1981), Evans (1972), Hunt (1978a, 1982), and Wall (1989).

**Yield Component Analysis**

Yield component analysis began in 1923 with Engeldow and Wadhams research on wheat and barley grain yield (Fraser and Eaton, 1983). This approach assumes that variation in yield is the result of variation among yield components. Many analytic approaches have been used for yield component analysis (Fraser and Eaton, 1983) and continue to be developed (Eaton *et al.*, 1986). Yield component analysis is beneficial in that it not only determines that there is yield variation but also determines the relative role of each yield component or stage in this yield variation as well as allowing each yield component to be tested against another.

Testing yield components against one another can establish correlations which are useful in establishing the mechanism of yield variability. Negative correlations reveal compensation whereas positive correlations suggest reinforcement. Compensation is not inevitable as increases in yield can occur without compensation (Eaton - personal communication).

**Sub-organismal Demographic Analysis**

This approach to growth analysis was introduced by Bazzaz and Harper (1977) who applied it to flax (*Linum usitatissimum* L.). Although their paper has been criticised (Hunt, 1978b) the technique itself is considered an important advancement to growth analysis. This
technique assumes that every organism consists of a population of structures that can be analyzed demographically. The general procedure is that plant components are tagged as they occur so that their chronology and relative contribution to final yield can be determined. One of the main advantages of this technique over conventional plant growth analysis is that by tagging there is less need for destructive harvesting. A good example of the utility of this technique for answering practical questions is the work of Lovett Doust and Eaton (1982) with beans.

Although growth analysis has been available and applied to crops since before 1920 the use of growth analysis for the study of weeds is a relatively recent innovation. Growth analysis is a tool that can, and should, be used by weed researchers to assist in understanding and explaining differences between treatments from a weed-centred perspective. Such understanding will lead to a more rapid understanding of weed biology and in turn, more effective weed management decisions.

**Allometry**

Allometry has been defined many ways (Gould, 1966) and generally refers to the growth relationship that exists among the different parts of an organism. A good overview of plant allometry is presented in Niklas (1994). Pearsall (1927) proposed a generalized model for an allometric relationship between plant parts of the form

\[ \theta_r = \beta \theta_p^\alpha \]
where $\Theta_i$ is plant part "i", $\Theta_p$ is plant part "p", $\beta$ is a scaler that equals $\Theta_i$ when $\Theta_p = 1.0$. The allometric exponent $\alpha$ represents the relative growth rate of $\Theta_i$ and $\Theta_p$ (Whitehead and Myerscough, 1962).

$$\alpha = \frac{R_i}{R_p}$$

Although many other functions could be used to describe allometric relationships the power function developed by Pearsall is the most accepted. Huxley (1932), even suggested that this function was a universal biological law for relating parts of an organism. Gould (1966) has demonstrated that this equation does work well in many instances.

Pearsall's power function and the methods used to derive the function and interpret the results have become accepted routine conventions (Smith, 1980). The dangers associated with the routine nature of the usage and interpretation of this function have been outlined. Smith (1980) demonstrated how some procedures are unnecessary or misleading and has proposed methodologies to avoid pitfalls. Seim and Sather (1983) demonstrated the importance of selecting an appropriate regression analysis for the objective of the allometric study particularly for data-sets with low correlation coefficients.

Allometry is of agronomic importance. Indices such as harvest index are simple allometric ratios and yield component analysis (Fraser and Eaton, 1983) often involves allometric relationships. Allometric relationships can be used in general modelling of plant productivity and in investigating the nature of interference (Whitehead and Myerscough, 1962; Jolliffe et al., 1988).
Vegetation Sampling

Properly conducted vegetation sampling enables a researcher to make inferences about a population by intensive examination of a only a small portion of the population. Choice of a sampling method depends on the goal of the survey, the morphology of the species, the spatial pattern of the species and the research resources available (Chapman, 1976). Additionally, sampling methods must be precise (able to detect population differences), accurate (truly reflect the population) and efficient (minimum cost).

Vegetation sampling usually is conducted for one of two goals; either to estimate a characteristic or attribute of a population (descriptive survey) or to explore relationships or test hypotheses (analytic survey) (Satin and Shastry, 1983; Ives and Moon, 1987). Analytic surveys are often conducted only after a descriptive survey of the population has been completed.

Quadrat Size, Shape and Numbers

Efficient vegetation sampling and analysis is in part dependent on proper quadrat selection. In vegetation surveys a quadrat is simply the sampling unit or portion of the population sampled. This sampling unit can be square, rectangular or circular (Knight, 1978).

A review by Van Dyne et al. (1963) determined that, in general, low perimeter-to-area ratios decreased accuracy because of edge effects and that perimeter-to-area ratios are lowest in circular quadrats. Bormann (1953) discovered that the best precision was obtained from rectangular quadrats because they encompass more heterogeneity per quadrat then square or
circular quadrats.

The best quadrat size is dependent on the morphology and homogeneity of the population being measured as well as the type of analysis that will be conducted on the collected data. If a population consists of regularly or randomly distributed clumps, and the size of the quadrat is much different from the mean size of the clumps of individuals, then the population will appear to be random, when in fact it is not (Elliot, 1977). Greig-Smith (1964) has suggested as a rule-of-thumb to use a quadrat that is twice as large as the mean canopy spread of the largest species. If the species being measured are at several scales, nested quadrats can be used with different sized quadrats fixed at the same sample site to sample each of the different scales of the hierarchy. Generally the choice of quadrat size is made subjectively by combining intuition and convenience.

From a statistical point of view, a general rule for sampling is 'the more the better' (Chapman, 1976). From a practical standpoint determining the number of samples is a matter of establishing a balance between statistical requirements and research resources available. As a rule of thumb, Knight (1978) indicates that to characterize a site at least 20 quadrats are required. A simple approach is to manipulate quadrat size and number so that a certain percentage, usually between 1 and 20%, of a stand is sampled (Chapman, 1976). Analytically the number of quadrats to use can be determined by intensively sampling a test site, plotting the running means (or some other statistic of interest), and assessing the point on the resulting graph at which additional quadrats yield diminishing returns (Knight, 1978; Nyrop et al., 1986). Alternatively one could sample until the standard error of the quadrat data is within some acceptable bound (Eckblad, 1991). The bound could be the standard
error of sampling, as it is usually desired that standard errors should be no more than 15-20%
of the mean (Menzies - personal communication). The bound could also be that the
variability within sample areas should be less than variability between sample areas (Chapman
1976).

**Survey Methods**

There are several survey methods that are commonly utilized to sample vegetation.
These survey methods are: representative; random; systematic (includes transects); stratified
(includes restricted random); and cluster (Chapman, 1978; Benoit et al., 1989).

In representative sampling, sampling units are arranged subjectively, usually to
selectively include special features. The subjectivity of this method induces bias that limits
statistical analysis except for some multivariate techniques such as ordination (Chapman,
1976).

In random sampling, a predetermined number of sampling units is selected in a way
that every unit in the population has an equal chance of being sampled. Because every
sample must have an equal chance of being sampled, by simply throwing a quadrat over ones
shoulder does not assure randomness (Chapman, 1976). A concern with random sampling
is that the population may not be uniformly sampled over the full range of the population
and the samples will not be representative.

In systematic sampling, a selection interval is used to determine where a sample unit
falls following a random start. This ensures increased population representation and in turn
results in relatively greater accuracy than achieved with random sampling. Transects are
simply a form of systematic sampling in which sample units are arranged linearly (Chapman, 1976). Accuracy of systematic sampled units can be a problem if the periodicity of the selection interval coincides with some natural periodicity (Satin and Shastry, 1983).

In stratified sampling, the population is subdivided into relatively homogeneous subdivisions called strata and every stratum is sampled with randomly selected sample units. This method usually involves laying out a grid defining strata boundaries although using a baseline with perpendicular transects and multiple starts can achieve the same effect. The goal of stratification is to increase precision by increasing population representation. Cochran (1977) indicates that no more than six strata are required as further subdivision leads to diminishing returns. Strata can be homogeneous on a proportional basis or on some optimization basis. Optimum allocation is usually used when allocation on a proportional basis will be unsatisfactory in increasing precision (Satin and Shastry, 1983). A simple form of stratified sampling is referred to as restricted random sampling (Chapman, 1976). In this simpler form, the population is simply subdivided on some subjective basis and each subdivision sampled at random.

In cluster sampling, a number of primary sample areas (clusters) containing several secondary sample units are selected randomly from a population. All secondary sample units within a cluster are then sampled. The main advantage of cluster sampling is that samples units are concentrated which can simplify sampling and, in turn, increase sampling resource efficiency (Satin and Shastry, 1983). Green (1979) has suggested that cluster sampling could be used for sampling strongly aggregated populations. A problem with cluster sampling is that neighbouring sample units within a cluster may have more characteristics in common
than the general population (strong autocorrelation). Optimum precision in cluster sampling is obtained when clusters are as heterogeneous as possible; this effect is the opposite of what occurs in stratified sampling (Stuart, 1976).

Information on sampling vegetation or general survey techniques has been compiled into a large number of comprehensive reviews or texts. The author recommends the following: Stuart (1976), Southwood (1976), Cochran (1977), Elliot (1977), Green (1979), Satin and Shastry (1983), and Ives and Moon (1987).

PLANT INTERFERENCE

Terminology

Interaction Types

Regardless of the means of interaction, species in mixture invariably affect the probabilities of one another exploiting some resource or being exploited or manipulated by some external agent.

Burkholder (1952) catalogued a list of ten biologically possible interactions between organisms, only seven of which were examined enough to be named. Each interaction is symbolically represented for its influence on each of two species in a mixture using $+$, $0$, and $-$, for stimulation, no effect, and depression, respectively. This symbolism allows for rapid definition of the various terms used for interactions between pairs of species. The six main interactions when two plants are in contact are: neutralism $(0,0)$; competition $(-,-)$; mutualism
(+,+); commensalism (+,0); amensalism (0, -); and parasitism, predation, herbivory (+,-). Connell (1990) has suggested that the term amensalism be changed to asymmetrical competition to reflect the way this interaction is discussed in the literature.

**Interference vs. Competition**

Often used in a loose fashion with little scientific basis, the term competition is frequently applied to agronomic phenomena (Hall, 1974a). Donald (1963) was among the first to come up with a relatively clear definition of competition:

"Competition occurs when each of two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate supply of the factor or thing is below the combined demand of the organisms".

Using this definition the term competition does not refer to all mutual relationships among neighbouring individuals, as the expression is commonly misapplied, but is applicable only to those specific relationships where individuals compete for a resource. The most recent weed science (Anonymous, 1985) definition of competition is:

"The reduction in supply of resources to one organism as a result of active acquisition by another".

Plants require the resources of light, water, nutrients, carbon dioxide and oxygen for growth and these are the resources over which plant competition may occur. Other plant-plant interactions which occur, such as changes in environment and allelopathy are non-competitive interactions (Harper, 1977).
Other researchers have classified competition into "real" and "apparent" competition (Holt, 1977). A plant may appear to be affected by another but in reality it is some other indirect interaction that has facilitated the response. Real competition occurs as a result of direct interaction or indirect interaction on a shared resource (exploitation). Apparent competition occurs as the result of indirect interaction by some shared enemy (Connell, 1990). For example one plant species may encourage increased predation on an adjacent species and as a result will increase. This increase might incorrectly be interpreted as the increasing species being more competitive than the other (Holt, 1984).

The term interference has been proposed to describe all mutual relationships between plants and encompasses competitive and non-competitive and apparent competition interactions. Harper (1961) was the first to propose a definition of interference with this meaning. He defined plant interference as:

"... the response of an individual plant or plant species to its total environment as this is modified by the presence and/or growth of other individuals or species".

Thus the term interference can be used to describe a broader range of interactions between individuals than can the term competition. For example, if a plant is affected by another through the production of toxins, changing the behaviour of predators, or affecting conditions such as temperature or wind, then the term interference is applicable and not the term competition.

It should also be noted that this definition of interference allows for beneficial interactions and not just the obstruction effect that is typically understood by interference. The management practice of intercropping is based on the concept that potential competitors
may also benefit each other. A good review of beneficence in plants has been composed by Hunter and Aarssen (1988).

**Considerations**

Weed management programs developed using the weed-centred approach will axiomatically focus on the weed population. The characteristics of the weed population are determined by the interaction of genotype and environment. The genotype determines the species potential for germination, growth, and reproduction as well as the species response to environment. The environment determines what proportion of the population survives and the variation among individuals in the population. In turn, population survival may be characterized in terms of proximity factors (Radosевич, 1987) and the population variability may be characterized in terms of structural distribution factors (Watkinson, 1986).

Proximity factors in combination with species characteristics and environment determine the structural distribution of a population. Many population attributes described by broad terms such as fitness or competitiveness are simply functions of the characteristic structural distribution, proximity factors, species composition and environmental qualities determined in a particular population. All these population characteristics ultimately determine the interference potential of a population. This authors interpretation of the interrelationships of these various population characteristics are illustrated in Figure 1.

Most of the techniques and analyses developed for the weed-centred approach have emphasized the role of proximity factors. The main reasons for the proximity emphasis are:
Figure 1. A generalized illustration of the interconnectiveness of various population characteristics towards determining a subpopulation’s ultimate potential for interference.
(1) the historical recognition of the importance of density in interference (Aldrich, 1987), (2) the central role of proximity factors in determining the interference potential of a population (Figure 1), and (3) the relative ease of manipulation of proximity factors for experimentation (Radocevich, 1987). The techniques and analytical approaches for quantifying the role of proximity factors in interference are the focus of this review.

**Proximity Factors**

The interference relationship between plants is dependent not only on the characteristics of the neighbours but also depends on the proximity factors of spatial position (arrangement) and concentration (density and proportion). Many models have been developed to deal with density effects, usually based on the reciprocal yield law of Shinozaki and Kira (1956), but few satisfactory models exist to deal with the effects of arrangement or proportions. Dealing with the influence of spatial arrangement in some quantitative manner is one of the major challenges to researchers modelling crop/weed interference (Radocevich, 1988). New quantitative approaches that might ultimately assist in overcoming this challenge are multivariate techniques such as those reviewed by Cormack (1979) or the use of fractal models (Sugihara and May, 1990).

- **Importance of Space.** Interference by capturing resources and depriving neighbours brings about a competitive advantage. Successful capture depends on distance from neighbours and size and activity of the neighbours. Ross and Harper (1972) determined that growth of individual seedling grasses was a function of the biological space available to each
plant where biological space was a defined not only by position but also by stage of growth.

Density is not the exclusive cause of yield variation. After reviewing the literature Benjamin and Hardwick (1986) concluded that space per plant typically only accounts for roughly 20% of the variation in plant size. The remainder was dependent on the size and activity of neighbouring plants. Research by Mack and Harper (1977) indicated that an individual reacts to the effects of its neighbours and not to the density of the population. Spitters (1983a and b) demonstrated the importance of species proportion by including it in his yield density model. Their model results suggest that the density of each species relative to the other influences the yield of both. Weiner (1982) states that plant plasticity and the importance of spatial pattern limits the use of density in describing a plant population. In addition to numbers, size, distance, age, species and angular dispersion are relevant factors.

Simulations by Firbank and Watkinson (1987) indicate that the role of local competition may almost be completely obscured as the result of differences in emergence times of neighbours. O'Donovan et al. (1985) have shown that the per cent yield loss in barley and wheat was dependent, at any constant wild oat density, on the wild oat emergence time. For every day wild oats emerged before the crop the yield loss increased three per cent whereas for every day wild oats emerged after the crop yield loss decreased by three percent.

Ford (1975), studying Tagetes patula in a lattice arrangement, was able to show that plants that emerged as dominant were regularly distributed whereas the population as a whole was non-uniform. He suggested that the dominant plants were only seriously affected by competition from other dominant plants. Benjamin and Hardwick (1986) have suggested
that the limiting factor for yield is not deployment of plant size but is resource utilization. Pitelka and Ashmun (1984) have stated that clonal plants have mechanisms for minimizing intraplant competition while allowing effective interclonal competition.

- **Domain Models.** Researchers have generally picked one of four assumptions when modelling density relations. The zone of influence of individual plants at various densities is assumed to be either non-overlapping, overlapping, unbounded or diffuse (Benjamin and Hardwick, 1986).

  Non-overlapping domain models generally assume that plants grow from emergence until they meet another plant whereupon expansion ceases and the domain occupied by each plant is proportional to its biomass. These non-overlapping zones of influence are usually drawn as tessellation polygons and are referred to as Dirichlet domains, Meijering cells, and Theissen or Voronoi polygons (Benjamin and Hardwick, 1986). Examples of this approach are the experiments and models of Mead (1966), Fischer and Miles (1973), Armstrong (1974), Slatkin and Anderson (1984) and Sutherland and Benjamin (1987). By studying the influence of eccentricity and abcentricity on growth of carrots, Mead (1966) was able to show that the shape of a polygon and the position of a plant within a polygon were less important than the area of a polygon. Subsequent research using cocksfoot, *Dactylis glomerata*, by Ross and Harper (1972) supported this observation.

  Results from experiments with cocksfoot by Ross and Harper (1972) indicate that the zones of influence of individual plants is diffuse with considerable overlap. Overlapping domain models generally assume that the zone of influence of a plant extends for some radius
out from each plant. The influence of neighbouring plants within the plants zone of influence is then described through some function. An example of this approach can be found in the studies of Mack and Harper (1977) on a population of dune annuals. Goldberg and Werner (1983) proposed a mathematical function that takes into account the diminishing effects of one or more distant neighbours. Benjamin (1993) has recently completed experiments which indicate that overlapping domain models are more appropriate than non-overlapping domain models in simulating competition.

Unbounded domain models assume that all plants affect all other plants within the population. This working hypothesis was used by Aikman and Watkinson (1980) when they developed a model which assumed that the growth of each plant is proportional to a crowding index determined from the growth rate of the entire population.

Diffuse population models assume that the immediate neighbours have no greater influence than distant neighbours. This hypothesis rarely, if ever, holds true for plants and is therefore considered to be purely theoretical.

- **Agricultural Studies.** In agriculture, interest in modifying plant arrangement or spacing practices has been limited because of the practical limits of the tools available for planting and management as well as good success with traditional practices. With changes in technology, such as new planter designs, changes in crop management approaches, such as targeting economic weed thresholds instead of clean fields, and changes in consumer/industry preferences for more uniform and higher quality products, the importance of spatial pattern is no longer simply a subject of curiosity.
Traditionally crop-weed interference studies have documented weed density while neglecting crop density. Neglecting crop density can be a problem as Hume (1985) has shown that in spring wheat crop density is an important component of weed competition. He determined that wheat density in adjacent quadrats varied as much as 25 plants per square meter and that under competition yield per plant as well as dry weight and tillering all decreased with increasing crop density.

Holiday (1963) investigated the influence of row width on the yield of wheat, barley, oats and rye. He determined that at a constant seed rate decreasing the row width below 7 to 8" generally resulted in an increased yield, whereas, increasing the row width above the 7 to 8" standard has generally resulted in a decreased yield. Donald (1963) states that there are benefits to be gained by maximizing the distance to the nearest neighbour casting shade and in minimizing the distance from the centre of the plant to any point in the soil. However he also states that cultural factors such as seeding precision, fertilizer placement, and weed control may mean that in many circumstances the advantages of precision planting may be obscured.

Rectangularity is the ratio of the distance between rows to the distance between plants in the row. Willey and Heath (1969) reviewed research on plant rectangularity and determined that in general as rectangularity increases by increasing seed rate, or row width, yield per area declined. Willey (1982) has stated that the ideal spatial arrangement is one in which there is equidistance between any given plant and its neighbours. He also states that the extent to which rectangularity affects yield depends on plant plasticity. He cites the example of sugarbeets which begin to suffer a loss if rectangularity exceeds 2:1 whereas
rectangularities of 6:1 are acceptable for most tillering cereals. Mead (1966) observed for carrots that as rectangularity was reduced product uniformity was increased.

Jagannath (1978) studied sorghum and finger millet planting arrangements and observed triangular planting arrangements to result in less competition than rectangular or square plantings. This observation was particularly noticeable at higher planting densities. He also observed that the rectangular pattern was slightly better than square planting only when the rectangularity ratio was in the 1:2 to 1:2.5 range. Using a purely mathematical approach Pant (1979) assumed that plants had zones of influence that were either plate-like, cylindrical or hemispherical. Irrespective of the zone of influence his calculations of packing fractions suggest that the most effective planting patterns in decreasing effectiveness were as follows: hexagonal arrangement, a square arrangement and finally a rectangular arrangement.

Walker and Buchanan (1982) noted that, at equal seeding rates, crops are generally more competitive with weeds when sown in narrower as compared to wider rows. This finding is consistent with the statement by Harper (1977) that competition between plants increases as the distance between plants decreases. Fischer and Miles (1973) used models to investigate the importance of spatial arrangement on weed-crop competition. Results from their study suggest that the most effective planting patterns for weed competition in order of decreasing effectiveness were as follows: triangular lattice, square lattice, hexagonal lattice, rectangular lattice.

Sakai (1957) sowed rice cultivars in a hexagonal arrangement around a central test plant. He determined that both the number and the arrangement of the various cultivars influenced the yield of the central plant. Harper (1961) studied interference in two annual
grasses. The arrangement of species was varied between treatments while density and proportions were kept constant. At the end of the experiment the yields of the two species differed significantly by arrangement. Lindquist et al (1994) grew oat plants at various angular arrangements in concentric circles around a target oat plant and observed that yield of the target plant differed significantly by arrangement. All these researcher observed that with increasing aggregation competition was reduced.

- **Impact of Aggregation.** Most studies of pattern in plant populations has revealed that purely random patterns are rare; some degree of aggregation is the norm (Taylor et al., 1978; Hutchings, 1986). Such aggregations may act on species to enable them to avoid competitive exclusion (Weiner, 1982). A clumped superior competitor is subject to heavy interspecific interference and leaves gaps for an inferior competitor.

Weed scientists often assume a uniform pattern of weeds (Hughes, 1990; Thornton et al., 1990). If the weed pattern is actually patchy this can lead to an overestimation of yield loss and over-encourage herbicide use. It has been determined that weed populations are usually aggregated and spatially variable (Thornton et al., 1990; Wiles et al., 1992; Mortenson et al., 1994). Hughes (1990) demonstrated that Cousens (1985) basic yield loss model predicts decreasing yield loss with increase variability (aggregation) of weed density, his explanation being that crop-weed competition becomes less and less as aggregation increases.

Brain and Cousens (1990) have suggested that assuming a regular distribution is not costly in terms of herbicide spraying decision making. The decision to spray or not to spray is usually made at low weed infestation levels and at low weed infestation levels weed
patchiness has less impact on yield loss than at heavy weed infestation levels. This assumption has generally been supported by the results of simulations by Wiles et al. (1992) on broadleaved weeds in soybeans.

**Plant Size**

- **Importance.** In agriculture, understanding the mechanisms of variation in plant size is important; important to consumers who want uniformity in produce and important to producers who want to maximize yields (Benjamin and Hardwick, 1986). In a crop-centred approach, size variation has not been a major concern because through agricultural practices of seed grading and uniformity in planting depths, timing and densities, size variation within crops has been reduced. However, in weed populations size variation is a major concern due to natural variability in characteristics such as seed vigour, size, depth of emergence and dormancy. In a weed-centred approach, weed population size variability makes understanding the mechanisms of variation in plant size particularly important.

- **Mathematical Expression.** Plant size hierarchies are typically summarized mathematically by their skewness or their Gini coefficient. Skewness indicates whether the frequency distribution is asymmetric and can be J-shaped (skew<0), L-shaped (skew>0) or bell-shaped (skew=0). The Gini coefficient (G) is a measure of size inequality; G=0 when all individuals are the same size and G=1 in a population of infinite size where all but one
of the plants is infinitely small. A good review of the value of these two mathematical methods for expressing the magnitude of size hierarchy can be found in Weiner and Solbrig (1984). The Gini coefficient and the more commonly used coefficient of variation (CV) give almost identical results (Kenkel, 1995, personal communication).

Given that the Gini coefficient and skewness values would be expected to increase with stronger competition it has been suggested that they could be used as measures of intraspecific competition (Rejamanek et al., 1989). Analysis of the results of competition between Japanese millet and tomato determined that the Gini coefficient and skewness were inferior to other methods of assessing intraspecific interference (Rejamanek et al., 1989).

**Distributions and Influencing Factors.** Koyama and Kira (1956) were among the first to publish results showing that although the frequency distribution of mass per plant was approximately normally distributed at emergence, as time progressed, the distribution becomes increasingly positively skewed (L-shaped). This skewed distribution consists of few large individuals and many smaller ones and is referred to as a size hierarchy (Weiner and Solbrig, 1984). Koyama and Kira (1956) suggested that the L-shaped distribution is the natural outcome of the exponential nature of plant growth and that it is simply enhanced by competition. When increased plant growth and increased competition occur in a complementary fashion this is referred to as "snowball" cumulation (Wilson, 1988). Bimodality can also occur where there is a uniform two-tiered canopy of large plants and small plants (Westoby, 1984).

Size hierarchy tends to develop more quickly in high density populations. Weiner and
Thomas (1986) determined that increases in density resulted in increased size inequality in fourteen out of sixteen relevant studies they reviewed. The two studies where there was no size inequality reported were unique in that the plants were grown from seed and studied for only a short period after emergence. Weiner (1988) later suggested that the difference occurred because early plant interference is two-sided (for nutrients), whereas late plant interference is one-sided (for light). One-sided asymmetric competition, where larger plants have a disproportionate effect on smaller plants, is the most common situation (Thomas and Wiener, 1989).

A plant population size hierarchy can develop as a result of several influences (Benjamin and Hardwick, 1986). Biotic influences on size inequality include herbivory, pathogens, parasites, age/stage, genetics and interference. Abiotic influences on size inequality include spatial differences in microclimate and resources.

Age is a primary determinant of size variation in populations (Ross and Harper, 1972; Firbank and Watkinson, 1987). A small difference in age can result in a minor size difference that over time is exaggerated through interference. For example it has been shown by some researchers that time of emergence was the major influence on final plant size in their experiments (Ross and Harper, 1972; Firbank and Watkinson, 1987). These observations are consistent with work by Gan (1994) in Manitoba who did field studies on the emergence and growth of red spring wheat plants grown from seed lots of large and small seed at various planting depths. He observed that Haun stage and yields of individual plants were strongly correlated with date of emergence. He also observed that the first plants to emerge averaged over 3 times the yield of those plants that emerged 7 to 9 days later.
Wilson (1988), based on results from partitioned pot studies with *Festuca* species, argued that the importance of initial advantage in size or establishment is not as great as many has stated. Initial competition advantage by size is simply an artifact of light competition and is less important for nutrient competition.

Weiner (1988) indicates that size variation due to age may be distinct from size variation due to other causes. A plant that is small because of its age will have a greater prospect of continued growth than a plant of the same size because of suppression by herbivory or disease.

In most herbaceous plants age and size are not synonymous (Ogden, 1970). Stage of growth may be more important in determining the fate of an individual plant, especially with perennials, than is absolute age (Hutchings, 1986). Gan (1994) studied red spring wheat and observed that Haun stage was a good indicator of the yield of individual plants in a population. Use of stages recognizes both the major changes in morphology and the differences in duration of time spent in each stage better than absolute age does.

Size variation can be due to genetic differences in plants. Genetic differences that result in small plants and in turn reduced fecundity or death of those plants may be offset by subsequent improved adaptation of the population as a whole (Antonovics and Levin, 1980). However, since genetic variability is only one of many potential causes of small size it is likely that significant selection pressure on the population as a whole would be rare.

When interference occurs between plants, dominance and suppression are major influences on the size hierarchy. This influence may not be to increase the size hierarchy. Interference may actually slow the development of the hierarchy by slowing growth (Turner
and Rabinowitz, 1983 (cited in Hutchings, 1986)). The 'interference slows growth' hypothesis has yet to be proven and has been labelled an inappropriate interpretation of skewness by Weiner and Solbrig (1984). Ross and Harper (1972) suggest that in a grass population they studied the low weights exhibited by late emerging plants were lower than would be expected from the reduction in growing period alone. They attributed the relatively lower weights to the earlier plants capturing "space" that was subsequently unavailable to later emerging plants. These findings are consistent with that of Gan (1994) who investigated the growth of red spring wheat plants in Manitoba populations and determined that a greater proportion of plants that emerged late were infertile.

Whereas population weight distributions become positively skewed over time, the height distribution either remains symmetrical or becomes negatively skewed (J-shaped) (Hara, 1984). With interference for light small plants etiolate to maintain the same height as larger plants. Continued insufficient light following etiolation can result in mortality. Hara (1986) has modelled plant size hierarchy as a functional process of interference using light interception and extinction.

In plant populations the development of size hierarchy is an important determinant of performance and survival of individual plants in the population. Small etiolated plants are subject to mortality resulting in self thinning.

**Self Thinning**

Despite its universal occurrence mortality is often assumed to be negligible or is ignored when yield density relationships are described. Density-dependent mortality or self
thinning is a common phenomena. For example, Gan (1994) observed an inverse relationship between uniformity of emergence and self thinning in red spring wheat populations. As a plant population grows and density increases the height distribution of plants within the population gradually changes from a relatively normal distribution to a skewed one consisting of many small plants and a few large plants (Obeid et al., 1967). Under the competitive conditions imposed by high population densities those plants under the most competitive stress, usually the smallest plants, will eventually die decreasing the population skewness (White and Harper, 1970). As the plants continue to grow the skewness of the height distribution eventually exceeds the plasticity capacity of the remaining plants under the competitive stress and more of the plants die.

- **Mathematical Expression.** Yoda et al. (1963), in experiments with buckwheat, determined that the relationship between per plant biomass ($\beta$) and stand density ($\delta$) could be expressed by an equation of the form

$$\beta = \kappa \delta^{-3/2}$$

where $\kappa$ is a constant. This equation can be represented in its log transformed form

$$\ln \beta = \ln \kappa - 1.5 \ln \delta$$

The basis for the exponent term being "-3/2" has not been scientifically proven although it is likely related to packing a three dimensional organism into a two dimensional area (Weller, 1987). As a population grows it eventually reaches the carrying capacity of the habitat. At the carrying capacity any increase in an individual plants biomass must be at the expense of
an equal amount of biomass in some other member of the population. At this stage as individuals grow the population undergoes self-thinning and there is a gradient of -1. Eventually self-thinning results only in an increase in surface area and no more shared volume. At this stage a -3/2 gradient develops. The -3/2 gradient has been determined to be widely applicable to many species (White, 1981) and the equation is often referred to as the -3/2 thinning law or power law.

- **Influencing Factors.** Site fertility and light intensity are two variables which have been shown to modify the -3/2 power law. Ford (1975) and White and Harper (1970) have demonstrated that as light intensity declines the gradient moves down towards -1. If the nutrient supply is increased the gradient is reached more rapidly but the gradient is not changed (Hutchings and Budd, 1981).

Researchers (Hutchings and Barkham, 1976; Hutchings, 1979) have demonstrated that clone forming perennial plants do not follow the -3/2 power law. In such plants each shoot is connected to other shoots and the translocation of carbohydrates and other materials is possible. In clonal plants shoot mortality does not occur until after maturation. Biomass accumulation in clonal plants stops just short of the point where density dependent mortality would occur (Pitelka and Ashmun, 1984). Inter-ramet interactions, such as competition for light, results in reduced spacial overlap (Kenkel, 1993). This indicates that in clonal plants the -3/2 power law limits clonal growth but does not result in mortality.

- **Criticisms.** Weller (1987) reanalysed much of the data from previous studies
supporting the self-thinning rule and indicates that the data do not support the power law. His major criticism against the power law is that density dependent mortality begins before a stand reaches the -3/2 gradient. An additional criticism is that the current definition of self thinning is too broad (Osawa and Sugita, 1989; Weller, 1990). Studies on self thinning must specify whether they are dealing with interspecific size-density relationships, the species boundary line or the dynamic thinning line. Ziede (1987) concluded that thinning lines could not be generalized as straight lines and was critical of many authors for their uncritical acceptance of the "rule". Lonsdale (1990) expanded on the critical reviews of Weller (1987) and Ziede (1987) and reached similar conclusions.

There have been yield-density models developed that incorporate density dependence (Watkinson, 1980; Firbank and Watkinson, 1985). Such models are more complex than required for most weed crop situations. With good field management, density dependent mortality should only be of minor importance.

**Approaches and Quantification**

**Experimental Designs**

Given that investigators have a wide range of interests when investigating plant interference it should be no surprise that several approaches have been developed to assess interference between species. Generally the only element in common between the various approaches is that each approach is a type of bioassay in which the response of one species is used to assess the influence of the other. The four main classes of experiments used to
assess competition in mixed stands are: additive, substitutive, systematic, and neighbourhood. Reviews of these experimental designs to assess interference are found in Oliver and Buchannon (1986), Radojevich (1987 and 1988), Snaydon (1991) and Sackville Hamilton (1994).

- **Additive Experiments.** Additive experiments are probably the most common approach used to study weed crop competition. In this approach an indicator species at a some fixed density is grown with a competitor species at a range of densities. Because it is only the density of one species that is varied this specific approach might more appropriately be called a partial additive design (Rejmanek et al., 1989). This approach has historically been the most widely used approach for assessing crop losses due to weeds (Zimdahl, 1980; Radojevich and Holt, 1984). It has the advantage of simulating what happens in weed-crop situations and therefore can be used to develop weed threshold levels at which crop loss justifies control measures. Implicit in this approach is the assumption that the single crop density used is optimum for both weedy and weed-free conditions.

The weakness of the additive approach is that interpretation of the competitive relationships that occur in an additive approach are confounded with concurrent changes in total population density and proportions (Harper, 1977; Firbank and Watkinson, 1985; Radojevich, 1987). Other associated criticisms include the assumptions that intraspecific competition remains constant, spatial arrangement has no influence, and that the technique is unable to distinguish between intra- and interspecific competition (Radojevich, 1987 and 1988). Snaydon (1991) has suggested that because overall density has no meaning the
criticisms of the additive approach are invalid.

- **Substitutive Experiments: Replacement Series Design.** Next to additive designs the use of a substitutive approach introduced by DeWit (1960) is probably the most widely used experimental approach for studying weed crop competition. In this approach, also referred to as a replacement series, the overall population density of a plot is kept constant while the proportion of the density allocated to each component species is varied from 0 to 100%. One key aspect of this approach is that monocultures of each species are included in the design. In this approach it is assumed that the plant population density chosen is beyond the point of constant yield (DeWit, 1960). The replacement series design was developed to overcome the confounding of density and proportions criticism of additive designs (Harper, 1977).

Harper (1977) and Inouye and Shaffer (1981) have criticised the replacement series design on its artificiality in that in natural infestations, populations will shift over time to densities not included in the original design. Radosevich (1988) has pointed out that the design can be cumbersome when the species have different life histories or growth forms. Mead (1979) criticised the technique for the confounding of density with spatial arrangement. Firbank and Watkinson (1985) criticised the design on the basis that it did not allow the prediction of the yield of both species to be estimated at any mixture proportion or density. Jolliffe et al. (1984) criticised the design on the basis that it did not allow the separation of competition into intraspecific and interspecific effects. Connolly (1986) has criticised the derived indices from replacement series designs because of their density dependence. He has
also determined that many of the commonly derived indices of competition from a replacement series experiment showed variability in results, indicating that replacement series experiments could lead to erroneous conclusions when researching competition.

- **Substitutive Experiments: Additive Series Design.** In order to maximize interpretation of replacement series designs it has been stated that monoculture data at a range of densities is required (Jolliffe et al., 1984). The importance of varying both total population density and frequency in mixtures has also been emphasized by Firbank and Watkinson (1985).

    One approach to address these suggestions is the additive series design. In this design several replacement series are combined over a range of densities in an additive fashion (Rejmanek et al., 1989). Snaydon (1991) considers an additive series design to be only those designs in which the densities of each component in mixture is identical to that which also occurs in pure stand. Additive series designs provide a balanced data set which is highly recommended for weed-crop competition studies (Rejmanek et al., 1989).

- **Substitutive Experiments: Diallel Design.** Mixture diallels are simplified versions of replacement series experiments that have been used by population geneticists for interference studies (Trenbath, 1974). In this approach a set of genotypes is grown in a 1:1 mixture of all possible pairs, including monocultures. The analysis of mixture diallel data provides information on both the productivity and aggressiveness of genotypes in mixtures compared
to monocultures. Trenbath (1978) has reviewed the interpretation of mixture diallel experiments.

The advantage of this design is its simplicity (Harper, 1977). The disadvantages of this design include its artificiality, since resources will be relatively nonlimiting with only one pair of plants per pot.

- **Systematic Experiments: Nelder Design.** As a way to determine optimum intercropping densities, Nelder (1962) devised fan-shaped 'systematic experiments' that have been modified to a parallel row approach by Blesdale (1967). With this approach plants are grown at a wide range of densities without changing the pattern of arrangement. These designs usually consist of plants arranged in a grid arrangement such that the amount of space available to each plant varies systematically over the different parts of the grid (Radosevich, 1987). This design maximizes the efficient use of experimental material by minimizing the amount of non-experimental area (Mead, 1979). The problem with systematic designs is they lack randomization which limits the statistical analysis that can be performed on the data collected. Additionally, only individual plants are measured, which means that the influence on a population is unavailable.

Radosevich (1987) has also criticized the Nelder design as it is normally conducted for allowing confounding of density and proportion effects. He has also criticized the design for not allowing partitioning of intraspecific and interspecific interference.

- **Systematic Experiments: Addition Series Design.** In his investigations on
intercropping Spitters (1983 a and b) developed a systematic approach called an addition series. The addition series is not a design, but instead it is a method of analysing data from mixtures grown in an ascending progression of total densities (Radojevich, 1987). This method has also been called a completely additive design (Rejmanek, 1989). The approach is based on using Spitters' (1983 a and b) multispecies reciprocal yield model to determine the yield of a species based on the densities available in the mixtures. Firbank and Watkinson (1985) used this approach for two species and were able to separate the effects of intra- and interspecific interference.

A criticism of this approach is that it does not account for spatial arrangement and that a lack of sufficient randomization can be a concern (Radojevich, 1987).

**Neighbourhood Experiments: Partitioning Design.** Several experimental approaches have been developed to provide physiological insight into the mechanisms and sites of interference between plants. Several designs are available that separate root and shoot interference for light and nutrients using separating panels in pot cultures (Schreiber, 1967; Evetts and Burnside, 1975; Snaydon, 1979; Wilson, 1988). Hall (1974 a and b) was the first attempt to integrate this approach with the DeWit (1960) approach. Snaydon (1979) developed a comprehensive approach that combines the complementary additive and replacement series experiments as well as allowing adjusting the relative density of species in soil and in aerial space. The main criticism of this approach is that interference is restricted in two dimensions and that the procedure creates artificial microclimate effects.
Neighbourhood Experiments: Proximity Design. When an investigator is interested in how the yield of an individual plant is affected by the presence of its neighbours a proximity neighbourhood approach may be appropriate. In this design the performance of an individual plant is recorded in relation to some characteristic of its neighbours. Most of these experiments have focused on the amount of neighbours (Mack and Harper, 1977; Weiner, 1982, Goldberg and Werner, 1983), whereas others have focussed on zones of influence (Bridges and Chandler, 1984; Gunsolus and Coble, 1986) or spatial arrangements (Silander and Pacala, 1985; Lindquist et al, 1994).

A criticism of neighbourhood models is that these approaches are usually based on the performance of individual plants and that variation in microsite quality can limit their usefulness, particularly at low densities (Waller, 1981).

A summary of the practical merits and limitations of the four major designs used to investigate weed interference are listed in Table 1.

Indices of Interference and Combined Yield

Indices are used to combine or summarize data. Many indices have been proposed to aid in the interpretation of the results of mixture experiments and no standard indices have been adopted for quantifying interactions in mixture experiments. The applicability and appropriateness of each index is dependent on the users objective. These objectives can range from elucidating the effects of density and proportion on plant interaction to the differentiation between intra- and interspecific interference.
### Table 1. Some of the practical relative merits and limitations of various general experimental approaches used to investigate weed interference.

<table>
<thead>
<tr>
<th>Merits</th>
<th>Limitations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Additive Experiments</strong></td>
<td>• Specific competitive relationships difficult to determine</td>
</tr>
<tr>
<td>• Directly applicable to the field</td>
<td>• Assumes intraspecific interference constant and spatial arrangement not important</td>
</tr>
<tr>
<td>• Easily conducted in the field</td>
<td></td>
</tr>
<tr>
<td><strong>Substitutive Experiments</strong></td>
<td>• Not directly applicable to practical weed problems</td>
</tr>
<tr>
<td>• Ideal for interference models</td>
<td>• Can be difficult to conduct in the field</td>
</tr>
<tr>
<td>• Good for use in greenhouse studies</td>
<td>• Confounds density and spatial arrangement</td>
</tr>
<tr>
<td>• Excellent for evaluating the role of proximity factors on competition</td>
<td>• Interpretation limited by density dependence</td>
</tr>
<tr>
<td><strong>Systematic Experiments</strong></td>
<td>• Difficult to plant and establish</td>
</tr>
<tr>
<td>• Good for intraspecific interference studies</td>
<td></td>
</tr>
<tr>
<td>• Guard plants only needed around outer edge of plants</td>
<td></td>
</tr>
<tr>
<td>• Allows study of a wide range of densities without changing pattern</td>
<td>• Not readily adapted to interspecific interference studies</td>
</tr>
<tr>
<td><strong>Neighbourhood Experiments</strong></td>
<td>• Variability between weeds can mask significance</td>
</tr>
<tr>
<td>• Effective for studying the influence of spatial arrangement on individual plants</td>
<td>• Critical germination timing and seed placement</td>
</tr>
<tr>
<td>• Good for computer models</td>
<td>• Focused on arrangement</td>
</tr>
<tr>
<td>• Utilizes little land area</td>
<td>• Not directly applicable to practical weed problems</td>
</tr>
</tbody>
</table>
Connolly (1986) has demonstrated that many of the indices used for interpreting the results of replacement series experiments developed prior to 1984 are limited in usefulness because of their density dependence. Changing pure stand density, and in turn pure stand performance, often will result in a change in index value.

Snaydon and Satorree (1989) have suggested that indices of interference and combined yield can be grouped into three categories: (i) indices of resource complementarity, (ii) indices of competitive ability, and (iii) indices of competition severity. To date these categorizations have not been widely adopted.

To facilitate cross-referencing of the indices described in this review a list of symbols used is provided in Table 2.

- **Dew's Index of Competition.** Dew (1972) developed an equation to predict potential crop losses by wild oats. It has subsequently been used by various researchers to assess yield losses in various crops by other weeds. It is of the form:

\[
Y_L = Y_{wi} \cdot (IC) \cdot \sqrt{N_j}
\]

Where \(Y_L\) is yield loss, \(Y_{wi}\) is the weed free yield, \(N_j\) is wild oat density, and IC is Dew's index of competition. With Dew's index of competition the larger the value the greater is the competition.

The IC is derived from an additive series by a simple regression of crop yield \((Y_i)\) on the square root of the population density of an associated weed \((N_j)\). The regression is of the form
Table 2. List of symbols used in formulae to derive indices of interference and combined yield.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Name or description</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Coefficient of aggressivity</td>
</tr>
<tr>
<td>a</td>
<td>Equation parameter</td>
</tr>
<tr>
<td>b</td>
<td>Equation parameter</td>
</tr>
<tr>
<td>CI</td>
<td>Competition index</td>
</tr>
<tr>
<td>CR</td>
<td>Competition ratio</td>
</tr>
<tr>
<td>d</td>
<td>Population density (plants per land area)</td>
</tr>
<tr>
<td>EF</td>
<td>Species equivalence factor</td>
</tr>
<tr>
<td>i</td>
<td>Subscript indicating plant species</td>
</tr>
<tr>
<td>ii</td>
<td>Subscript indicating plant species i in monoculture</td>
</tr>
<tr>
<td>Ij</td>
<td>Subscript indicating plant species i and j in mixture</td>
</tr>
<tr>
<td>IC</td>
<td>Index of competition</td>
</tr>
<tr>
<td>j</td>
<td>Subscript indicating plant species</td>
</tr>
<tr>
<td>jj</td>
<td>Subscript indicating plant species j in monoculture</td>
</tr>
<tr>
<td>ji</td>
<td>Subscript indicating plant species j and i in mixture</td>
</tr>
<tr>
<td>k</td>
<td>Subscript indicating variable at point where Y is 50% of ( Y_{\text{max}} )</td>
</tr>
<tr>
<td>K</td>
<td>Relative crowding coefficient</td>
</tr>
<tr>
<td>Kc</td>
<td>Index of competitive ability</td>
</tr>
<tr>
<td>L</td>
<td>Subscript indicating loss</td>
</tr>
<tr>
<td>LER</td>
<td>Land equivalent ratio</td>
</tr>
<tr>
<td>m</td>
<td>Subscript indicating monoculture</td>
</tr>
<tr>
<td>max</td>
<td>Subscript indicating maximum</td>
</tr>
<tr>
<td>N</td>
<td>Number of plants</td>
</tr>
<tr>
<td>NDI</td>
<td>Niche differentiation index</td>
</tr>
<tr>
<td>p</td>
<td>Subscript indicating projected in absence of interference</td>
</tr>
<tr>
<td>RC</td>
<td>Relative competitive ability</td>
</tr>
<tr>
<td>RM</td>
<td>Relative monoculture response</td>
</tr>
<tr>
<td>RX</td>
<td>Relative mixture response</td>
</tr>
<tr>
<td>RY</td>
<td>Relative yield</td>
</tr>
<tr>
<td>RRT</td>
<td>Relative resource total</td>
</tr>
<tr>
<td>RYT</td>
<td>Relative yield total</td>
</tr>
<tr>
<td>Ty</td>
<td>Reciprocal of maximum theoretical y</td>
</tr>
<tr>
<td>x</td>
<td>Subscript indicating mixture</td>
</tr>
<tr>
<td>y</td>
<td>Yield per plant</td>
</tr>
<tr>
<td>Y</td>
<td>Total yield per land area or variable</td>
</tr>
<tr>
<td>Z</td>
<td>Sown proportion of a species (in mixture)</td>
</tr>
<tr>
<td>u</td>
<td>Theoretical maximum ( Y_{ij} )</td>
</tr>
</tbody>
</table>
\[ Y_i = a_i - (b_{ij}) \sqrt{N_j} \]

where \( b_{ij} \) is the regression coefficient and the IC is simply the ratio of \( b_{ij} \) over \( a_i \). This index has been determined useful for studying the competitive abilities of crops against weeds (Dew and Keys, 1976).

There are two assumptions in the IC that limit its utility. The IC assumes that the weeds and crops emerge at the same time and it also assumes that crops and weeds have equal access to resources.

- **Relative Crowding Coefficient.** One index of mixture productivity is the relative crowding coefficient (K) of DeWit (1960). It is calculated for two species mixtures as follows:

\[
K_i = \frac{(1-Z_i) / (y_{yi}/(y_{ij}))}{Z_i} - Z_i
\]

\[
K_j = \frac{(1-Z_j) / (y_{yj}/(y_{ij}))}{Z_j} - Z_j
\]

\[
K_{ij} = K_i \times K_j
\]

The species are said to crowd for the same space if the product \( (K_{ij}) \) is 1.0. If the product is larger than 1.0 then the species are said to crowd only partially for the same space. If the product is smaller than 1.0, then one species interferes with the other through some means other than crowding (Willey, 1979a).

- **Competition Index.** McIntyre (in Donald, 1963) formulated a competition index
(CI) for a species grown in mixture. The CI is based on the calculation of equivalence factors for each species in mixture. For any species "i" the equivalence factor (EF) is the number of plants of "i" required to be as equally competitive as one plant of species "j". This is established by determining what monoculture plant number (Nj) is required to give a comparable yield per area (Yij) in the mixture. The CI is then calculated as follows:

\[ \text{CI} = (\text{EF}_i \times \text{EF}_j)/(\text{Z}_i \times \text{Z}_j). \]

When the CI is less than 1.0 there is minimal competitive interference and the mixture over yields. The major problem with this approach is that a large number of monoculture population densities are required to estimate equivalent plant numbers (Willey, 1979a).

- **Coefficient of Aggressivity.** An index of aggressiveness of one species towards another is that of McGilchrist and Trenbath (1971) called the coefficient of aggressivity (A). It is calculated for two species as follows:

\[ A = \left( \left( \frac{y_{ij}}{y_{ji}} \right) - \left( \frac{y_{ji}}{y_{ij}} \right) \right) / 2 \]

A high positive value indicates that "i" is aggressive and a high negative value indicate that "j" is aggressive. The greater the numerical value, the greater the difference in competitive species ability (Willey, 1979a). Because this index incorrectly assumes that yield changes are exclusively related to competitive ability the index has been shown to give inconclusive results in practice (Hall, 1974b; Willey and Rao, 1980).
- **Competitive Ratio.** Another index of the aggressiveness of one species towards another is the competitive ratio (CR) of Willey and Rao (1980). The CR simply the ratio of the individual relative yields of the two component crops. It is similar to the coefficient of aggressivity but corrects for the proportion in which the crops were initially sown. This allows for a direct comparison of values. It is calculated for two species as follows:

\[
CR = \frac{y_{ij}}{y_{ii}} / \frac{y_{ij}}{y_{jj}}
\]

Intensity of competition is easily quantified using the CR. For example a CR of 2 indicates that \(i\) could be regarded to be twice as competitive as \(j\). Willey and Rao (1980) have suggested that this index could be useful for identifying plant characteristics that are associated with competitive ability.

- **Relative Yield Total / Land Equivalence Ratio.** As an index the relative yield total (RYT) of DeWit and Van den Bergh (1965) is one of the most stable. It is an index that is used to describe the productivity of pairs of species that have access to the same resources. It is simply the sum of the relative yields (RY) for each species. It is also sometimes referred to as the land equivalent ratio (LER) (Willey and Osiru, 1972). It is calculated for two species mixtures as follows:

\[
RY_i = \frac{Y_{ij}}{Y_{ii}}
\]

\[
RY_j = \frac{Y_{ji}}{Y_{jj}}
\]

\[
RYT_{ij} = RY_i + RY_j
\]

Values of RYT near 1.0 indicates that the two species are interfering with one another.
A RYT greater than 1.0 implies that the species are showing some kind of amensalism either by making different demands on resources or having a symbiosis. A RYT less than 1.0 indicates that there is some kind of antagonism between the two species (Willey, 1979a).

For a replacement series, the LER is identical to the RYT. The RYT by definition is limited to replacement series designs whereas the LER can be applied to both additive and replacement series designs. Mead (1986) has recommended that the term RYT be restricted to use in replacement series designs whereas the term LER should be restrictively used for agronomic studies. Mead and Riley (1981) have reviewed the various methods used to calculate the LER and have presented some statistical concerns with this method.

- **Relative Resource Total.** All the indices discussed previously are based on the performance in mixture relative to the performance in pure stand. A difficulty arises in that pure stand performance is likely different than that in mixtures. Connolly (1987) has proposed a new index that overcomes this density dependent weakness. It is called the relative resource total (RRT) and is based on the assumption that whether in mixture or in pure stand the amount of resources required to produce an individual of given size is the same. The relative resource total is an index of whether species are capturing the same amount of resources in mixture as in pure stand. The relative resource total for two species in mixture is calculated as follows:

\[ \text{RRT} = \frac{d_{ij}}{d_i} + \frac{d_{ji}}{d_j} \]

Where \(d_{ij}\) is the density of 'i' in mixture (where per plant yield = 'a'), \(d_i\) is the
density of 'J' in mixture (where per plant yield = 'b'), \( d_i \) is the monoculture density when 'i' per plant yield = 'a', and \( d_j \) is the monoculture density when 'J' per plant yield = 'b'.

A RRT of 1.0 implies that the mixture does not yield more than an equivalent proportioned combined pure stand configuration. A RRT greater than 1.0 implies that the mixture utilizes more resources or is utilizing existing resources more efficiently. A RRT less than 1.0 implies reduced resource use in the mixture or some antagonism. A RRT of 2.0 or greater indicates that there is no competition between the individuals for resources and higher values suggest some synergistic effect in the mixture.

- **Index of Competitive Ability.** The index of competitive ability (Kc) was proposed by Jolliffe et al. (1984) as a measure of competitiveness of species in a specific mixture. The values obtained are inversely related to the effectiveness of one species interfering with another. (i.e. the larger the value the less the interference). It is calculated as follows:

\[
K_c = \frac{(d_k \times d_i \times Y_{ij})}{((u \times d_i) - (d_i \times Y_{ij}) - (d_k \times Y_{ij})}
\]

Where \( d_k \) is the planting density at which \( Y_{ii} = u/2 \), \( d_i \) is the planting density of species i, \( u \) is the theoretical maximum yield at infinite planting density, \( d_j \) is the planting density of competing species j, \( Y_{ij} \) is the yield per land area of species i in mixture, where \( Y_{ii} \) = monoculture yield of species i.

\( K_c \) is an index that is not based on the density dependent replacement series monoculture yield but is based on a standardized expected monoculture yield density (Kz).
The weakness of this index is that it is based on the theoretical, and thus arbitrary, maximum monoculture yield (u).

- **Relative Competitive Ability and Niche Differentiation Index.** When species are partly limited by the same resources they partially avoid each other; this is referred to as niche differentiation. A measure of the degree of niche differentiation between two species is the niche differentiation index (NDI). The NDI is simply the product of the reciprocal yield ratios for each species. The reciprocal yield ratios comes from the reciprocal yield analysis approach of Spitters (1983a) where regression equations are used to describe the relationship of the mean individual plant yield to the density of each species. The regression equation for each species used is of the form:

\[
\frac{1}{y_i} = \frac{1}{Y_i} + (b_{i1} \times N_i) + (b_{i2} \times N_j)
\]

Where \( \frac{1}{y_i} \) is the reciprocal of the mean yield/plant of species \( i \) (i.e. Reciprocal Yield), \( \frac{1}{Y_i} \) is the reciprocal of the maximum theoretical yield/plant, \( N_i \) is the density of species \( i \), \( N_j \) is the density of species \( j \), \( b_{i1} \) is the parameter reflecting intraspecific competition, \( b_{i2} \) is the parameter reflecting interspecific competition.

The parameters \( b_{i1} \) and \( b_{i2} \) can then be used to calculate the relative competitive abilities (RC) and NDI for each species as follows:

\[
RC_i = b_{i1} / b_{i2}
\]

\[
NDI = RC_1 \times RC_2.
\]
In a wheat and rye grass interference experiment, Roush et al. (1989) compared the relative utility of the relative yield total, reciprocal yield, and relative monoculture and relative mixture response to assess interference. They determined that the reciprocal yield approach was the simplest method for assessing the relative importance of intra- and interspecific competition in addition to it being the most sensitive to density and proportion in mixtures.

**Relative Monoculture and Relative Mixture Response.** Jolliffe et al. (1984) has proposed a density independent method that determines indices of interspecific and intraspecific competition. This approach has also been referred to as the synthetic no-interaction approach by Roush et al. (1989). A detailed description of the model used to calculate these indices is found in Jolliffe (1988). They have proposed that the yield response to density is of the form

\[
1/Y = 1/Y_{\text{max}} + (d_k/Y_{\text{max}})(1/d)
\]

Where \( Y \) is the yield per unit area, \( Y_{\text{max}} \) is the maximum yield or final yield constant, \( d = \) plant density, and \( d_k \) is the density at which 50% of \( Y_{\text{max}} \) is achieved.

A line of projected yield (\( Y_{\text{p}i} \)) expected if there was no intraspecific or interspecific interference can then be determined as follows:

\[
Y_{\text{p}i} = (Y_{\text{max}}/d_k)(d).
\]

They proposed that interpretation of data from replacement series data should involve comparisons among actual mixture yields (\( Y_{X_i} \)), actual monoculture yields (\( Y_{M_i} \)) and
projected monoculture yields \( (Y_{pi}) \). The difference between \( Y_{pi} \) and \( Y_{mi} \) would represent the effect of interspecific interference. That difference over the \( Y_{pi} \) denominator is called the relative monoculture response index (\( RM_i \)).

\[
RM_i = \frac{(y_{io} - y_{ii})}{y_{io}}
\]

The difference between \( Y_{mi} \) and \( Y_{xi} \) represents the effect of interspecific interference. This difference over the \( Y_{mi} \) denominator is called the relative mixture response index (\( RX_i \)).

\[
RX_{ij} = \frac{(y_{ii} - y_{ij})}{y_{ii}}
\]

In a wheat and ryegrass interference experiment Roush et al. (1989) comparing the relative utility of the relative yield total, reciprocal yield, and relative monoculture and relative mixture response to assess interference. They determined that the relative monoculture and mixture response approach provided the most detailed analysis of the influence of proportion on interference.

**MODELLING**

**Terminology**

A model is an abstract expression of the features of an object or system. A mathematical model is an equation or set of equations which attempts to represents the behaviour of a system (France and Thornley, 1984). Simulation is the art of taking a model and using it to perform experiments to study the properties of a system under study (DeWit, 1982). Good reviews of the philosophical basis of modelling can be found in Baker and

Models are described using various terms depending on whether a model is being classified by its purpose or by the attributes of the system being modelled or by the attributes of the model itself.

When a model is classified by its purpose it is described as either descriptive (empirical) or explanatory (mechanistic) (Penning de Vries, 1983; France and Thornley, 1984; Cousens et al., 1987). Empirical models are simple descriptions of data or response whereas mechanistic models incorporate perceived knowledge of underlying processes.

When a model is classified by the attributes of the system being modelled it is described as either discrete, continuous or spatial (Cousens et al., 1987; Edelstein-Keshet, 1988). A discrete model is one that reflects a system that occurs in stages. A continuous model refers to a system that is viewed as continuous in time. A spatial model indicates a system that has surface coverage as an important component.

A model can be classified by the attributes of the model itself and classified in terms of model output as either deterministic or stochastic and in terms of model parameters as static or dynamic or in terms of mathematical approach as either analytic or simulation (Anderson, 1972; Hall and Day, 1977; France and Thornley, 1984). A deterministic model makes a definite prediction of some value whereas a stochastic (probabilistic) model is one that predicts a value and gives some indication of its variance. Static models do not have time as a parameter whereas dynamic models do contain a time parameter. As a generalization analytic models represent systems in the language of mathematical formulae whereas simulation models estimate solutions using computer language (Knepell and Arangno,
1993).

In a comprehensive review, Cousins et al. (1987), categorized models into one of three classes: short-term (discrete), long-term (continuous), other (spatial).

Modellers develop models with differing degrees of refinement depending on the availability of data and the modellers goal. As the mathematical foundation for their models, modellers use whatever is convenient for their goal, whether simple or linear algebra or differential calculus or mathematical programming. As long as the model closely mimics and foretells the relevant features of the system under study it does not matter what mathematical approach is taken. The only rule of thumb is that simplicity and consistency of approach is preferred over complexity and inconsistency.

Evaluation

Having defined the problem, collected the data and developed the model the next step is to evaluate the model. Models are generally evaluated on two major criteria; practicality and mathematical soundness.

Models are usually developed with one of three purposes in mind: advancing science; predicting correct results; or instructing people (Penning de Vries, 1977). An ideal model will achieve all three purposes by being realistic, workable and communicatable. A realistic model will provide realistic results over the range of real world situations to which it might be applied. A workable model will use readily accessible input data and hardware. Models should be communicatable by being of a form easily understood and utilized by the end user.

Establishing the mathematical soundness of a model is predominantly a process of
verification, validation and sensitivity analysis (Anderson, 1972; France & Thornley, 1984).

Verification (model truthfulness) is the process of determining whether a hypothesis used in a model is correct. Verification is used in model evaluation when the model contains an untested hypothesis. Verification of a model is actually verification of a hypothesis and is often achieved by experimentation. Applying a predictive model to independent data and evaluating how close the model output reflects the actual output is one method of verification. Verification of a model is not possible if a system has information that is scanty or absent.

Validation (model usefulness) is the process of determining whether the model represents the system for which it is intended. For some models the correlation coefficient is a measure of how effective a model is in representing the system. Applying a model to some independent data and evaluating how well the model reflects this system is another method of validating a model.

When model optimization is a goal, sensitivity analysis is often used to evaluate a model (Anderson, 1972; Penning de Vries, 1983). Sensitivity analysis is the testing for the robustness of parameters and structures. It is a form of behaviour analysis where the value of a single parameter or group of parameters is changed within a reasonable range and the output is compared with what is expected. When the models output is relatively insensitive to changes in model structure or parameters then the model is considered robust. Testing for this robustness and ranking sensitivities enables the modeller to determine where any further model refinements are best concentrated.

However described or calculated, mathematical models are important tools
complementing experimentation. Modelling complements experimentation by forcing succinct mathematical expression of response, revealing knowledge gaps and allowing interpolation and cautious extrapolation in the absence of data (Cousens et al., 1987).

**Models of Intraspecific Interference**

Interference among plants involves the response of plants to the presence or growth of neighbouring plants. When the neighbouring plants are of the same species this monoculture interference is termed intraspecific. As the proximity between neighbouring individuals is reduced the interaction between individuals intensifies. In monocultures, except when plants are small or widely spaced, total plant yield is independent of density.

When the yield of individual plants in monocultures is considered there is a dependence on density. Holiday (1960) was the first to recognize that there are two basic monoculture yield density relationships. He recognized monoculture yield density relationships can be either asymptotic or parabolic. An asymptotic yield-density relationship usually occurs when yield is a measure of a vegetative trait and a parabolic yield-density relationship when yield is a measure of some reproductive characteristic.

A large number of models have been used to describe yield-density relationships and many of them have been compared in a review by Willey and Heath (1969). They singled out reciprocal yield models such as those proposed by Bleasdale and Nelder (1960) as showing the best promise for describing yield density relationships.

Much of the early work on intraspecific interference was done by Japanese researchers on several crop species and published in a series of papers from 1953 to 1957 (Kira et al.,
1953; 1954; 1956; Ikusima et al., 1955; Hozumi et al., 1955; 1956; Shinozaki and Kira, 1956; Koyama and Kira, 1956; and Yoda et al., 1957). Kira et al. (1953) were the first to demonstrate an asymptotic relationship between shoot dry weight and population density. This relationship was expressed mathematically by Shinozaki and Kira (1956) in a reciprocal model of the following form:

\[ y_i^{-1} = a_i + b_{ii}X_i \]

Where \( a_i \) and \( b_{ii} \) are constants, \( y_i \) is the per plant yield and \( X_i \) is plant density. To account for parabolic yield density relationships this equation was extended to its quadratic form by Holiday (1960).

\[ y_i^{-1} = a_i + b_{ii}X_i + b_{ii}X_i^2 \]

Willey (1982) has determined this quadratic equation to describe experimental data well despite its empirical nature.

Bleasdale and Nelder (1960) proposed a more flexible version of the Shinozaki and Kira (1953) reciprocal model that could describe both asymptotic and parabolic yield density relationships. Based on the Richards’ function (Richards, 1959) it was of the form:

\[ y_i^{-\theta} = a_i + b_{ii}X_i^{\theta'} \]

where \( \theta \) and \( \theta' \) are constants. Bleasdale (1967) later demonstrated that it was possible to take \( \theta' \) as unity and thus the reciprocal yield-density equation took the final form:

\[ y_i^{-\theta} = a_i + b_{ii}X_i \]

This model has been used to describe both parabolic and asymptotic yield-density
relationships (Jolliﬀe, 1988; Bleasdale, 1967). Although originally developed as an empirical model biological meaning has been ascribed to the parameters in the model (Shinozaki and Kira, 1956; Jolliﬀe, 1988). Parameter \( a_i \) may be considered an index of plant yield in the absence of interference. Parameter \( b_i \) is a factor expressing the responsiveness of a species to changes in its own density. Parameter \( \theta \) has been related to the eﬃciency of resource acquisition and utilization (Watkinson, 1980, 1984; Jolliﬀe, 1988) and its value determines the form of the yield density relationship. When \( \theta=1 \) the model describes an asymptotic curve and when \( \theta<1 \) the model describes a parabolic curve.

A criticism of the Bleasdale (1967) model is that except when \( \theta=1 \) there is no clear biological meaning to the equations parameters (Willey and Heath, 1969; Gillis and Ratkowsky, 1978; Watkinson, 1980). To address this deﬁciency Watkinson (1980, 1984) choose to reparameterize the Bleasdale Model to the following form:

\[
y_i = y'_i (1 + a'_i X_i)^{-b'_i}
\]

This model was derived by setting \( a' = a^{-1} b, b' = \theta^{-1}, \) and \( y' = a^{1/\theta} \). In this model Watkinson interprets \( y'_i \) as the yield of an isolated plant, \( a'_i \) is the minimum density at which interference becomes important and \( b'_i \) is the eﬃciency of resource utilization.

The monoculture yield-density models are of agronomic importance. Quantitative yield-density relationships are useful for determining optimum crop population density, in general purpose modelling of crop productivity, and for determining many of the indices used to analyze plant performance in mixtures.
Models of Quackgrass Intraspecific Interference

Intraspecific interference modelling in quackgrass has been limited to the work of Mortimer and coworkers (Mortimer et al., 1980; Mortimer and Putwain, 1981; McMahon and Mortimer, 1980). They indirectly modelled quackgrass interspecific interference using a sophisticated modelling approach. Using a transition matrix (Leslie matrix), which included quackgrass survivorship and fecundities, they were able to analyze net reproductive rates and project quackgrass infestation levels in subsequent years. In their model system they determined that an annual mortality level of 73.7% was required to keep their model quackgrass population static and that an annual mortality of 99.2% was required to enable eradication (Mortimer et al., 1980). Mortimer was able to incorporate density dependent elements by making selected elements of the matrix functionally dependent on population density.

Models of Interspecific Interference

DeWit (1960) was the first to introduce a descriptive model of interference between two species. Subsequently Baeumer and DeWit (1968) developed a simulation model to predict interference between two species. Spitters and Van den Bergh (1982) then extended the Baeumer-DeWit model to crop weed relations. Since DeWit's (1960) descriptive model was proposed many descriptive indices have been proposed and these are discussed in the indices of interference and combined yield section of this literature review.

Spitters (1983) took the reciprocal yield-density model for monocultures of Bleasdale (1966, 1967) and extended to a multispecies hyperbolic equation of the form:
\[ y_{x_i}^{-1} = a_i + b_{ix}X_i + b_{ij}X_j \]

In this model \( Y_{x_i} \) is the derived mixture per plant yield variable mean, \( a_i \) is the parameter that is related to the scale of the yield variable in the absence of competition, \( b_{ix} \) is a model parameter related to the extent of intraspecific interference, \( X_i \) is the population density of species "i", \( b_{ij} \) is a model parameter related to the extent of interspecific interference and \( X_j \) is the population density of species "j".

Firbank and Watkinson (1985) modified the Spitters (1983) equation to a form that accounts for mortality. Their approach presents a pair of equations for each of a pair of species in mixture. The equations for a species "A" are as follows:

\[ W_A = W_{mA} \left( 1 + a_A \left( N_A + \beta N_B \right) \right)^{-ba} \]

and

\[ W_A = W_{iA} \left( 1 + m_A \left( N_A + \delta N_B \right) \right)^{-1} \]

By substituting \( B \) for \( A \), and \( A \) for \( B \), in the equations the formulas could be applied to species \( B \). In the equations shown \( \delta \) and \( \beta \) are competition parameters describing the effect of species \( B \) on the yield and survival of species \( A \). \( N \) is the number of plants at harvest. \( W_m \) is the mean yield of isolated plants. Parameter \( a \) is the area required by a plant to achieve a yield equal to \( W_m \). The parameter \( b \) is a measure of the efficiency of resource utilization by the population.

Jolliffe (1988) modified the Spitters (1983) equation to a form:
\[ y_{xi} = a_i + b_iX_i + b_jX_j \]

which is more flexible. The model parameter \( \Phi_i \) is related to the efficiency of resource utilization and determines whether the response function will be hyperbolic or parabolic. Many of the commonly used weed-crop loss models including the Firbank and Watkinson (1985) model presented earlier and Cousens (1985) hyperbolic model

\[ y_{xi} = aX_i / (1 + bX_i + fX_j) \]

and the exponential model of Gill et al. (1987)

\[ y_{xi} = (a + be^{-Ky}) / X_i \]

can be demonstrated to be reparameterized versions of Jolliffe's (1988) model.

There are two potential criticisms of all these models. They assume population size is normally distributed and they assume that intraspecific competition is the same in monoculture as in mixture. As discussed previously these assumptions are only rarely valid.

**Models of Quackgrass Interspecific Interference**

Interspecific interference by quackgrass has often been monitored, but only rarely modelled. The literature contains many reports of the estimated yield losses associated with particular quackgrass infestations. Cussans (1970) investigated quackgrass competition between quackgrass and barley, wheat and field beans and reported that their yields were unaffected by low infestations of quackgrass but a population of 180 shoots m\(^{-2}\) reduced yields as much as 20 \%. Quackgrass has been found to reduce the stem diameter of sweet corn by 42\% and ear yield from 26.5 kg to 6.1 kg per 100 plants (Bouchard and Doyon,
1983). In field corn, quackgrass at densities of up to 390 shoots m\(^{-2}\) caused yield reductions up to 16% and densities up to 900 shoots m\(^{-2}\) were observed to cause yield losses of 37% (Young et al., 1984). In soybeans yield reductions due to quackgrass averaged up to 1% for infestations up to 160 shoots m\(^{-2}\) and 19% to 55% for heavy infestations of 520 and 910 shoots m\(^{-2}\) respectively (Young et al., 1982). In potatoes, Baziramakenga and Leroux (1994) determined that quackgrass infestation influenced marketable yields more than total tuber yields and that yields losses were positively correlated with infestation level and interference period. For example, at one site, when left weed free for 10, 20 and 30 days after emergence, marketable potato yields were reduced by 35%, 14%, and 11%, respectively.

Quackgrass interspecific interference in barley and wheat in Quebec has been modelled using linear regression. The relationship between quackgrass shoot density m\(^{-2}\) (Qs), approximately 30 days after planting, and predicted crop yield as a percentage of the expected quackgrass free crop yield (Y\(_{i}\)%), was determined in barley, by Rioux (1982), to be of the following form:

\[ Y_{b}\% = 100 - 0.16 \times (Qs), \quad R^2=0.80. \]

In wheat, Leroux (1990) determined the regression to be of the following form:

\[ Y_{w}\% = 100 - 0.48 \times (Qs), \quad R^2=0.60. \]

These models estimate that at a quackgrass infestation of 100 shoots m\(^{-2}\) that the predicted crop yields would be 84 and 52% of their quackgrass free yields for barley and wheat, respectively.

Interspecific interference between annual crops and quackgrass has also been modelled
using a rectangular hyperbola. O’Donovan (1991) reported that yield loss in polish canola
(\textit{Brassica rapa}) in Alberta was related to quackgrass shoots m\(^{-2}\) as follows:

\[ Y_c \% = 100 \left\{ 1 - 0.41 \left( \frac{Qs}{100} \right) / 100 \left( 1 + (0.41 \left( \frac{Qs}{141} \right)) \right) \right\}, R^2 = 0.66. \]

Chikoye (1990) reported that flax (\textit{Linum usitatissimum} (L)) grown in Manitoba could be
related to quackgrass shoots m\(^{-2}\) as follows:

\[ Y_f \% = 100 \left\{ 1 - 2.07 \left( \frac{Qs}{100} \right) / 100 \left( 1 + (2.07 \left( \frac{Qs}{130} \right)) \right) \right\}, R^2 = 0.42. \]

In preliminary reports from this thesis (Wilcox and Morrison, 1988a; Morrison \textit{et al}, 1990)
it has been determined that the relationship between percentage wheat yield and quackgrass
shoots m\(^{-2}\) in Manitoba was of the following form:

\[ Y_w \% = 98.7 \left\{ 1 - 0.433 \left( \frac{Qs}{100} \right) / 100 \left( 1 + (0.433 \left( \frac{Qs}{193.7} \right)) \right) \right\}, R^2 = 0.41. \]

These models estimate that at a quackgrass infestation of 100 shoots m\(^{-2}\) that the predicted
crop yields would be 47, 0 and 46\% of their quackgrass free yields for canola, flax and wheat,
respectively.

Rauber (1984) conducted a replacement series experiment with mixtures of winter
wheat and quackgrass. Using the DeWitt competition model and crowding coefficients he
was able to demonstrate that wheat was less impaired by quackgrass than was the growth of
quackgrass by wheat.

Fawcett (1985) used a complex quackgrass management model (AGROMOD) to
model the impact of various management practices on quackgrass infestations. This matrix
model included a density dependence component. After using this model to simulate effects
of crop rotations, soil tillage and herbicide application, it was observed that the relative
competitiveness of the crop was a major factor in controlling quackgrass infestations.

**QUACKGRASS**

Quackgrass is a long-lived herbaceous perennial weed that spreads both by seed and an extensive underground rhizome system. Rhizomes are white or light buff, long, branching, slender, smooth surfaced and very sharp-pointed, with many nodes each containing a scale leaf and bud or branch and a fine root system (Palmer and Sagar, 1963). Culms can be up to 120 cm tall and typically have three to five nodes. Leaves are flat 5 to 13 mm wide and 6 to 30 cm long. Auricles are short and clasping with sheaths rounded on the back and a membranous, narrow, flat-topped ligule. Spikes are erect, with numerous wedge-shaped overlapping spikelets. Spikelets are 3 to 8 flowered, alternating in two rows on opposite sides of the axis flat-wise to the rachis. The caryopsis is tightly enclosed by a hard lemma and palea. The lemmas and glumes may have awns. (Palmer and Sagar, 1963; Werner and Rioux, 1977). As a self-sterile, polyploid species (Stebbins, 1950) quackgrass infestation is often the result of vegetative reproduction from rhizome segments. However, the ability of quackgrass to express genetic variation through seed production contributes to it's environmental adaptability.

Until relatively recently, quackgrass was most often referred to by the species name *Agropyron repens* (L.) Beauv. (Scoggan, 1978). Authorities now generally refer to quackgrass by the species name *Elytrigia repens* (L.) Nevski. (Love, 1984; Dewey, 1984) although some
taxonomists argue that *Elymus repens* (L.) Gould (Melderis, 1978) would be more appropriate.

Quackgrass is notorious for being one of the most difficult weeds to manage in many agricultural areas of the northern temperate zone (Holm *et al.*, 1977). Quackgrass commonly grows in open disturbed areas (Werner and Rioux, 1977) and although able to grow on a wide range of soils it seems to prefer well-drained to medium textured soils (Dale *et al.*, 1965). Native to southern temperate Europe, it has followed European settlers and travellers to almost every part of the temperate world. Quackgrass was probably first introduced to North America around 1672 in the Boston region of New England and to Canada near Prescott, Ontario in 1861 (Alex, 1987). Quackgrass was first reported as occurring in Manitoba in 1906 (Alex, 1987). Of the 4.4 million acres of wheat now grown in Manitoba it is estimated that quackgrass occurs in 11% of the fields with a mean mid-season density of 10.4 shoots m⁻² (Thomas and Donaghy, 1991).

Effective quackgrass control requires a combination of control methods. Crop rotations, tillage, and use of graminicides are the major management approaches to consider for quackgrass control. Crop rotations work by taking advantage of the differing ability of crops and specific crop management practices to influence quackgrass infestation. Recent research by Pessala (1981) and Harker and O'Sullivan (1993) has demonstrated that crop selection does influence long-term infestation densities of quackgrass. By 'shredding' or 'dragging-out' quackgrass rhizomes, appropriately timed tillage operations can reduce quackgrass infestation levels. However, care must be taken with tillage operations not to spread quackgrass rhizome segments to new regions of the field. A large body of literature confirms that as cultivation is reduced quackgrass infestation increases (Bachthaler, 1974;
Cussans, 1975; Donaghy and Stobbe, 1972; Harker et al., 1986; Mueller-Warrant and Koch, 1980; Nielson and Pinnerup, 1982; Pollard and Cussans, 1976; Stobbe, 1978). However, other researchers (Derksen et al., 1993) have determined that reduced cultivation does not mean increased quackgrass infestation. Control of quackgrass by graminicides can range from poor to good, depending on the graminicide and application conditions. Herbicides recommended in Manitoba for quackgrass control include glyphosate, quizalofop-ethyl, sethoxydim, clethodim, and fluazifop. Glyphosate is listed as providing 'good' control as a pre-harvest treatment, whereas the previously listed post-emergent products are listed as providing only 'fair' control (Anonymous, 1995). A review of quackgrass control with graminicides and factors affecting their activity is presented in Harker (1987) and Harker and Dekker (1988a and b).

More thorough descriptions of quackgrass biology and control can be found in the following reviews: Palmer and Sagar (1963), Frankton and Mulligan (1971), Werner and Rioux (1977), Holm et al (1977), Glick (1987) and Chikoye (1990).

SYNTHESIS

Assessing interference in mixtures of plants can be done either through surveys or through experimental investigation. In interference research the characteristics of plants and populations can be measured and summarized through indices or models to indicate the influence of interference on plant growth.
Radosevich (1987) has suggested that the important factors involved in plant interference should be considered and controlled in interference studies or else varying results, sensitivities, and interpretations will occur. He specified that proximity factors should be controlled. Harper (1977) has stated that in addition to the easy to manipulate proximity factors, other factors such as the environment, emergence characteristics, growth rates and other components of plant size and function are also important influences on the interference process. Plant interference researchers need to recognize and account for the relative importance of all relevant factors (Figure 1) to the outcomes of their experiments and or analysis. With such recognition the interference researcher can optimize experiments or surveys to be as comprehensive as possible, so that as far as practical all relevant factors are measured and documented.

From a weed science perspective, once the factors that influence the process of interference are understood, weed suppression methods can be developed with greater certainty as to their impact both in terms of weed control and crop yield.