International Journal of Biosciences (IJB)
ISSN: 2220-6655 (Print) 2222-5234 (Online)
Vol. 1, No. 5, p. 1-17, 2011
http://www.innspub.net

REVIEW PAPER OPEN ACCESS

Yield-density equations and their application for agronomic research: a review

Ibrahim Yahuza

Crops Research Unit, Department of Agriculture, the University of Reading, Reading RG6 6AR, United Kingdom

Received: 04 August 2011
Revised: 15 August 2011
Accepted: 15 August 201

Key words: Yield-density equations, asymptotic response, parabolic response.

Abstract

Plant population density (density) trials are time consuming, repetitive and cost intensive. The literatures indicate that density trials are more effectively and efficiently described when meaningful yield-density equations such as reciprocal linear and/or parabolic equations are applied to quantify data. Several of these types of equations and their derivatives such as competitive indices have been proposed. It is generally agreed that where response to density deviated from linearity, equations based on linear reciprocal of yield per plant and density can satisfactorily describe an asymptotic response. In certain cases when the harvest index is substantially affected by density and/or due to unfavourable growth conditions, equations that assumed parabolic responses may be more valid. The review by Willey and Heath (1969) on the quantitative response of yield to density appears to have remained a useful resource up to date. However, more recently, several investigations based on reciprocal quantitative relationships between yields and density and how this may be influenced by other agronomic practices were carried out. Yet, most of these substantial knowledge and progress on yield-density investigations appear to be scattered in published or unpublished works as no attempt has been made to collate them together. This paper reviews more recent progress on yield-density equations research and their application, and highlights needs for the applications of some of these equations for agronomic research with more emphasis given to intercropping.

Corresponding Author: Ibrahim Yahuza ✉ yiahmed@yahoo.co.uk

Introduction

In most cases, plants in a crop start to compete with neighbouring plants after emergence, because the seed sowing density is often adjusted to maximize the yield (Bleasdale, 1966a; Firbank and Watkinson, 1985). Crops compete for nutrients, water and light (Helenius and Jokinen, 1994; Law and Watkinson, 1987; Li and Watkinson, 2000).Yield-density relationship can be literally defined as a mathematical quantification of crop response to increase in plant population density (henceforth often referred simply to as density) (Bleasdale, 1967; Li and Watkinson, 2000). The use of equations in density trials for determining optimal density for the sole crop and density combinations for the intercrops is more efficient than analysis of variance procedures alone (Ellis and Salahi, 1997). This is because establishing the quantitative relationships between two or more variables using mathematical equations helps to reduce the need for multi location density trials and it is possible to extrapolate beyond actual data (see Willey and Heath, 1969; Spitters, 1983; Connolly, 1987). In any case, maximum yield for any plant in a crop may be achieved at that density of plants at which competition with the plant is minimal (Helenius and Jokinen, 1994; Shirtliffe and Johnston, 2002). Often the growers or researchers are interested in yield of a crop rather than yield of a plant in a crop. In general provided growth conditions are favourable, yield of a crop increases linearly as density increases as more plants are occupying space that would have been left vacant and/or occupied by weeds (Firbank and Watkinson, 1985; Rejmanek *et al.*, 1989). In such cases yield can be simply quantified using a linear function (Equation 1). However, it should be emphasised that most of the asymptotic equations reviewed here are applicable mainly where yield is solar driven (Willey and Heath, 1969). In other words in situations where water and nutrients are not the major limiting growth resource.

$$Y = a + bp \qquad 1$$

Where a and b are constants whilst p is density.

However, this may not hold indefinitely. So yield can be quantified more appropriately using a quadratic function of the type described by Equation 2.

$$Y = a + bp + cp^2 \qquad 2$$

Where a, b and c are constants whilst p density.

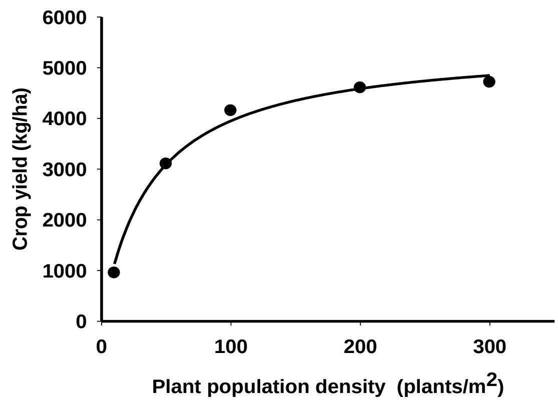

Fig. 1. An illustration of general pattern of asymptotic increase in crop yield per unit area as the density (p) is increased ; the filled cycles are the observed data (●) and the solid curve (———) is described by Equation 4 derived by Shinozaki and Kira /Holliday, 1960b (After Willey and Heath, 1969; Bleasdale, 1984).

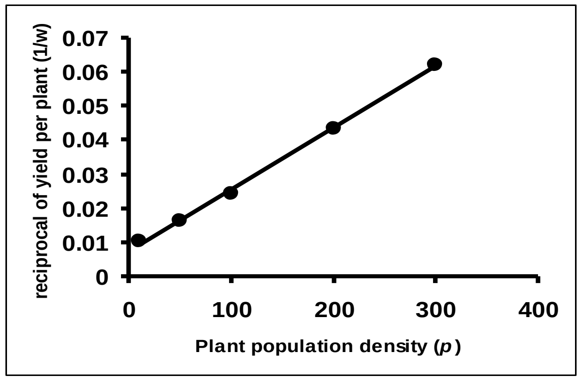

Fig. 2. An illustration of general pattern of the response of reciprocal of yield per plant (1/w) to density (p) where the area yield density relationship is asymptotic; the filled cycles are the observed data (●) and the solid line (———) is described by Equation 3 according to the assumptions of Shinozaki and Kira /Holliday, 1960b (After Willey and Heath, 1969; Bleasdale, 1984).

The literature indicates that Equation 2 has no meaningful biological interpretations and is less efficient in describing yields satisfactorily (see Willey and Heath, 1969; Mead, 1970). In situations where yields responded quadratically to increase in density, it is documented that applying either an asymptotic and/or a parabolic equation is biologically more appropriate (Bleasdale, 1966a, b; 1967; Counce, 1987; Khah *et al.,* 1989; Ellis *et al.,* 1999).

The peculiarity of intercrops is that plants might compete for growth resources with neighbours of both the same and at least one different crop species (Ofori and Stern, 1987; Francis, 1989; Watkinson and Freckleton, 1997; Park *et al.,* 2002). Yield-density equations and their applications are as relevant in the analysis of ecological data as it is to applied science of intercropping. However, in this paper the term intercropping is used to refer to both mixture experiments in ecology and intercropping in agronomy. In intercropping investigations, the term intra-specific competition is usually used to describe the competition between plants of the same crop species (Vandermeer, 1989; Tollenaar, 1992; Helenius and Jokinen, 1994). On the other hand, the term inter-specific competition is used to describe the competition between plants of different crop species in an intercrop (Freckleton and Watkinson, 1997; Watkinson and Freckleton, 1997). There is a general agreement that when inter-specific competition for a given limiting factor is less than inter-specific competition among plants for that same factor there is a potential for high total production in the intercrop (Vandermeer, 1989; Innis, 1997; Park *et al.,* 2002). Fukai and Trenbath (1993) ascribed the term dominant to refer to the most competitive component whilst the term dominated refers to the suppressed component. It is interesting to note that for intercropping, modified versions of the biologically meaningful asymptotic and parabolic equations have been developed (e.g. Wright, 1981; Helenius and Jokinen, 1994). The modified equations were meant to account for the peculiarities of intercropping where both intra-specific and inter-specific competition exists (Watkinson, 1981; Dolman, 1985; Park *et al.,* 2002). Indeed, several equations, their derivatives and competitive indices with meaningful biological interpretations have been proposed and some of these equations are reviewed in this paper.

Yield-density relationships

In the introductory section it was pointed out that at low densities, the relationship between density and yield is typically linear (Willey and Heath, 1969; Heath, 1970; Shirtliffe and Johnston, 2002). As competition begins as the density is increased, the relationship usually deviates from linearity such that the gradient declines until yield plateaus or subsequently declines (Holliday, 1960a, b, c; Counce, 1987). The situation where crop dry matter yield becomes relatively stable at higher densities has been described as asymptotic (Bleasdale, 1966a, b; 1967; 1984). On the other hand, the situation where a decline in crop yield occurs at the highest densities as the density is increased further is parabolic (Willey and Heath, 1969; Counce, 1987).

Earlier, several attempts were made to establish the relationship between crop yield and density before the work of Shinozaki and Kira (1956) as cited by Willey and Heath (1969). It is not within the scope of the present paper to go into details of some of the earlier equations that have been used to study yield-density relationships. Willey and Heath (1969) have reviewed in detail previous attempts at quantifying the relationship between crop yield and density. They concluded that the equations based on the reciprocal relationships between yield per plant and densities were better than other equations. Therefore, details of the earlier equations are not presented in this paper. However, it should be stressed that density trials are more efficiently described using the modelling approach for both the sole crop (e.g. Counce, 1987; Ellis and Salahi, 1997; Shirtliffe and Johnston, 2002) and intercrops (e.g. Wright, 1981; Dolman, 1985;

Helenius and Jokinen, 1994; Park *et al.,* 2002). In other words, applying biologically meaningful equations has been adjudged the most appropriate approach in determining optimum density or density combinations (for the intercrops). In the subsequent sections, several of these equations are presented. In any case, throughout the paper, Y represents yield per unit area, w represents weight per plant and p represent density. Where subscripts and/or superscripts are used, they would be defined subsequently in the appropriate sections of the paper.

Reciprocal equations

The reciprocal equations have been widely accepted as being better in giving a truly asymptotic or parabolic fit to data accurately and meaningfully (Bleasdale, 1984). Shinozaki and Kira (1956), first described the use of reciprocal equations to describe the relationship between crop yield and density mathematically, but it was Holliday (1960a, b) whose study (independent to that of Shinozaki and Kira) demonstrated the existence of the relationship empirically (Willey and Heath, 1969). The reciprocal equations can quantify asymptotic or parabolic relations (Bleasdale, 1984; Khah *et al.,* 1989; Li and Watkinson, 2000). The simplest form of reciprocal equation (asymptotic equation) was derived from a simple logistic curve and the law of constant final yield (see Willey and Heath, 1969). The approach was developed because geometric equations were deficient in satisfactorily fitting an asymptotic yield-density curve (Willey and Heath, 1969). According to the assumption of the equation, a linear relationship exists between the reciprocal of yield per plant (1/w) and density (p) as is described by Equation 3 (Bleasdale and Nelder, 1960; Holliday, 1960a, b, c; Mligo and Craufurd, 2007).

$$1/w = a + bp \qquad 3$$

Given that yield per unit area (Y) is a function of yield per plant (w) multiplied by the density (p) (i.e. wp), Equation 3 can be inverted and then multiplied by p as described.

$$Y = \frac{p}{a + bp} \qquad 4$$

In Equations 3 and 4, Y = yield (g/m²), a and b are constants (constant 'a' is related to yield of a plant in a competition free environment whilst constant 'b' is related to maximum yield potential of the environment (see Willey and Heath, 1969), and p refers to density (plants/m²).

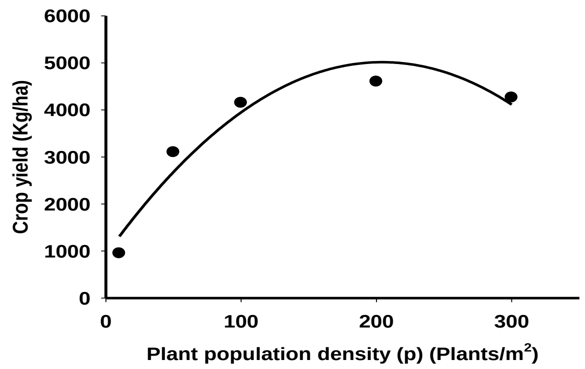

Fig. 3. An illustration of the general pattern of parabolic increase of crop yield per unit area as the density (*p*) was increased ; the filled cycles are the observed data (●) and the solid curve (———) is described by Equation 6 derived by Holliday, 1960b (After Willey and Heath, 1969; Bleasdale, 1984).

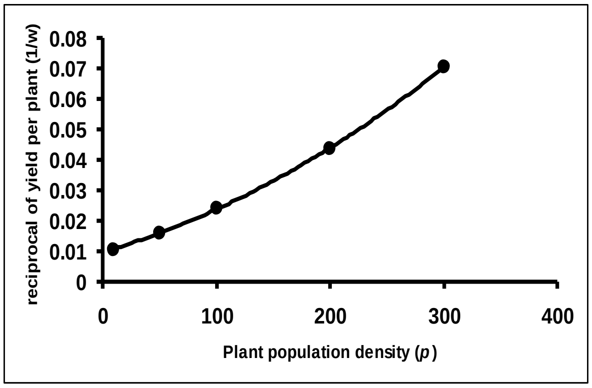

Fig. 4. An illustration of the general pattern of the reciprocal of yield per plant response to density where the area yield-density relationship was parabolic; the filled cycles are the observed data (●) and the solid curve(———) is described by Equation 5 according to the assumptions of Holliday, 1960b (After Willey and Heath, 1969; Bleasdale, 1984).

Conversely, a curvilinear relationship is assumed between the reciprocal of yield per plant (1/w) and density (*p*) in parabolic situations where a decline in yield occurs at high density (Bleasdale and Nelder, 1960; Bleasdale, 1966a, b; 1967; Counce, 1987).

Reciprocal equations describing asymptotic yield-density relationship

Equations 3 and 4 derived by Shinozaki and Kira (1956) and which Holliday (1960a, b) developed independently can describe asymptotic yield-density relationships satisfactorily (Mead, 1979; Mligo and Craufurd, 2007). Fig. 1 gives an illustration of a typical asymptotic curve, and Fig. 2 shows diagrammatically the response of the reciprocal of mean yield per plant to density where the yield-density relationship is asymptotic (Willey and Heath, 1969; Bleasdale, 1984). If the asymptotic equation applies to seed yield, then the harvest index was not substantially influenced by density (Khah *et al.,* 1989; Craufurd, 1996; Gooding *et al.*, 2001; 2002) and the crop is not adversely affected by unfavourable conditions such as pest and diseases (e.g. Counce, 1987) .

Reciprocal equations describing parabolic yield-density relationship

In situations where the relationship between the reciprocal of yield per plant (1/w) is no longer linear with increase in p, the asymptotic yield-density relation does not hold (Bleasdale, 1984; Counce, 1987; Gooding *et al.,* 2002). Holliday (1960b) asserted that both asymptotic and parabolic yield-density relationships exist. He argued that the asymptotic form applies to the biomass dry matter yield and the parabolic applies to seed dry matter yield. In addition to the identical equation he derived to that of Shinozaki and Kira (1956), Holliday (1960b) proposed that the parabolic yield-density situations where the relationship between the reciprocal of yield per plant and density deviates from linearity could be described by a quadratic expression of the type described by Equation 5.

$$1/w = a + bp + cp^2 \qquad 5$$

Similar to Equation 3, this can be inverted and then multiplied by p as described thus

$$Y = \frac{p}{a + bp + cp^2} \qquad 6$$

In Equations 5 and 6 a, b and c are constants (see Willey and Heath, 1969; Counce, 1987).

Willey and Heath (1969) stated that Equation 5 provides flexible parabolic yield-density curves which are not symmetrical about the point of maximum yield and which flatten off realistically at high densities.

Where the parabolic relationship holds, Fig. 3 shows typical parabolic area yield-density relations and Fig. 4 show the response of the reciprocal of the mean yield per plant to density where the yield-density relations was parabolic. Previously it was widely accepted that the dry matter of the reproductive forms of yield (seeds) usually assume parabolic responses as the density was increased (Holliday, 1960c; Willey and Heath, 1969). However, several crops with reproductive yield have been demonstrated recently to assume asymptotic yield-density relationship. Indeed, such was the case for wheat (*Triticum aestivum*) (e.g. Pinyosinwat, 2001). While this facts were demonstrated empirically, it is the view of the writer that the assumption that for a given crop, yield-density relationship is generally asymptotic or parabolic might be misleading because other factors (adverse) other than density (e.g. pest infestation or diseases, weather variables) might control yield more than the main effect of density (Holliday, 1960b; Counce, 1987).

Biological basis for the reciprocal equations

The biological foundations for the reciprocal equations are well reviewed (see Willey and Heath, 1969). Hence, they will not be discussed in detailed here. However, it should be interesting to note that the asymptotic equations (Equations 3 and 4) which Shinozaki and Kira (1956) and Holliday (1960a, b) developed independently were derived from combining the law of constant final yield and the logistic curve (Farazdaghi and Harris, 1968; Heath, 1970). The biological validity of the equations is based on the assumption that the mean yield per unit area increases towards (1/b) which is the asymptotic yield (i.e. maximum yield attainable) as the density is increased (Shainsky and Radosevich, 1992; Helenius and Jokinen, 1994; Mligo and Craufurd, 2007). Given that the asymptote of yield per area is a measure of the potential of a given environment, it follows that b is a meaningful factor that defines environmental potential (Willey and Heath, 1969; Craufurd, 1996; Watkinson and Freckleton, 1997).

Conversely, as the density is decreased mean yield per plant increases towards (1/a) which is the yield of an isolated plant or a plant in a competition-free environment (Helenius and Jokinen, 1994; Pinyosinwat, 2001; Mligo and Craufurd, 2007). This suggests that the constant 'a' defines the genetic potential of the crop (Willey and Heath, 1969; Firbank and Watkinson, 1985; Tollenaar, 1992; Craufurd, 1996). However, Dolman (1985) observed that in reality, this cannot be true because competition ceases at a finite density p_o, below which the equation has no meaning. However, he concluded that p_o would in practice be sufficiently low for constant 'a' to have a dominant effect on the yield, so it probably has some connection with genetic potential of the plant. However, he reiterated that it is possible to have differences in the value of this constant when yield-density relationships are compared from different spatial arrangement, since the density at which competition ceases is lower with a less favourable spatial arrangement.

It has also been suggested that a/b is the 'relative' responsiveness to density. (Gooding *et al.*, 2001). These authors argued that the ratio will be greater for crop species with lower plasticity to decrease in density (low 1/a), but good at capturing and partitioning resources to the seed where density is high (high 1/b).

Application of the reciprocal equations in sole cropping

The need to apply reciprocal equations for agronomic research has long been recognised (e.g Holliday, 1960c; Bleasdale, 1966a, b; 1967). Therefore, it is not surprising that the reciprocal equations have gained acceptance among researchers because they are able to describe asymptotic, parabolic or both situations satisfactorily (e.g. Counce, 1987). Several authors have applied the equations to quantify either the biomass or the seed yields or both in several crop species (e.g. Khah *et al.,* 1989; Ellis *et al.,* 1999; Shirtliffe and Johnston, 2002). Indeed, in wheat, the yield of N in the seed appears to vary asymptotically with density in a similar way to the yield of dry matter (Gooding *et al.*, 2001). Gooding *et al.* (2002) applied Equation 4 to describe wheat biomass and seed dry matter yields as well as the intercepted photosynthetically active radiation (PAR) (in some experiments) satisfactorily. It is well documented that seed yields is a function of biomass yields and harvest index (HI) with the biomass yields in turn being a function of the PAR and the radiation use efficiency (RUE) (Giunta *et al.,* 2009). Whilst Equation 4, which has density, has the main variable can be easily applied to quantify seed yields, biomass yields and the PAR, it cannot be applied to the HI and RUE because they are not necessarily affected by density (see Azam-Ali and Squire, 2002). Therefore, my view is that the equation and its derivatives would have greater importance in quantifying seed yields, biomass yields and PAR in density trials. Similarly, Craufurd (1996) applied Equations 3 and 4 to quantify the effect of density on both the seed and biomass dry matter yields in a short-duration cowpea (*Vigna unguiculata*) cultivar grown in contrasting environments in the tropics. It is worth noting that despite the different environmental differences, the equations quantified the responses satisfactorily for both the biomass and seed dry matter yields. Mligo and Craufurd (2007) recently studied yield-density relationships in pigeon pea (*Cajanus cajan*) in contrasting environments and reported that Equations 3 and 4 fitted the responses of both the biomass and seed yield satisfactorily. These various investigations clearly indicate that Equations 3 and 4 are increasingly been applied in density trials.

Kindred and Gooding (2004) reported parabolic yield-density response of wheat when nitrogen was withheld. Counce (1987) on the other hand demonstrated the existence of both asymptotic and parabolic response of rice (*Oryza sativa*) yield to density. The fact that Counce (1987) demonstrated in his studies both asymptotic and parabolic responses of rice yield to density reemphasises that it is misleading to generalize the form of yield-density relationship that should be ascribed to any one-crop species. Counce (1987) contended that that where Equation 4 holds, then a critical or optimum density exists that can be determined as the density necessary to obtain 99% of the predicted yield (optimum yield) at the maximum density of an experiment

$$p_{crit} = \left(a0.99y_{\max}\right) \Big/ \left(h - b0.99y_{\max}\right) \qquad 7$$

Where h is a unit dependent constant (h = 1 when yield and density are expressed on the same area basis), a and b are as defined previously in Equation 3 and 4. ymax (for an experiment with an asymptotic response to p) is predicted yield at the maximum density, p_{crit} is population at 0.99ymax (Counce, 1987).

In practice, Equation 7 has not been applied widely in density trials. However, recently Mligo and Craufurd (2007) applied the equation successfully but with slight modifications. There may be a need to apply this equation to determine optimum yields in studies where Equation 3 and 4 apply. Craufurd (2000) had earlier applied the equation in an intercropping situation. However, as is discussed in a subsequent section this equation has limitation with respect to some intercropping designs. This clearly indicates that a modification may be required if the equation were to be used more widely for intercropping research.

It is worth noting that Equations 3 and 4 had also been extended to quantify the combined effects of density and applied nitrogen in spring-sown wheat using Equations 8 and 9 (see Ellis *et al.,* 1999; Salahi, 2002)

$$1/w = a + bp - cN \qquad 8$$

And hence

$$Y = \frac{p}{a + bp - cN} \qquad 9$$

In Equations 8 and 9, Y, w, a, b and p are as defined in Equations 3 and 4 whilst c is a parameter to define the effects of applied nitrogen (N, kg nitrogen/ha).

However, in their winter experiment quantifying yields using Equations 8 and 9 did not worked well mainly because of a curvilinear relationship found between 1/w and N (see Ellis *et al.,* 1999; Salahi, 2002). Thus, these equations were further modified to quantify yields using Equations 10 and 11.

$$1/w = a' + b' p - c' p \log 10N \qquad 10$$

And hence

$$Y = \frac{p}{a' + b' p - c' p \log 10N} \qquad 11$$

In Equations 10 and 11, Y, w, a', b' p, c' and N and are similar to definitions given to Y, w, a, b and p in Equations 8 and 9, even though the log presence in Equation 10 and 11 indicates the relatively complex nature of these relationships compared to Equations 8 and 9 (see Ellis *et al.,* 1999; Salahi, 2002).

However, to date none of these equations (i.e. Equations 8-11) has been applied by others in yield-density studies despite the fact that they have practical relevance in quantifying the combined effects of density and applied nitrogen, which is arguably the most limiting nutrient for crop production (e.g. Counce, 1987; Ellis *et al.,* 1999). For instance, it is well documented that applied nitrogen has substantial effects on canopy size and duration, PAR and yields (Kindred and Gooding, 2004). Besides nitrogen, it is possible to quantify the combined effects of density and other macro and even micronutrients on yields using these equations. This clearly indicates the relevance of these equations for agronomic research up to date.

Given the repetitive nature of density trials, an alternative approach that is based on the relationship that exists between the amount of dry matter accumulated by a crop and its transpiration (i.e. water lost from plant surfaces), over the same period has been developed. The approach helps to determine the appropriate density theoretically for a particular crop at any specified location (see Azam-Ali and Squire, 2002). Although this approach has not been applied widely. However, Azam-Ali *et al.* (1993) demonstrated the validity of the approach in determining the productivity and optimum p for groundnut crops grown across several locations in India. Here no details on these equations were provided. Azam-Ali and Squire (2002) documented details of this approach to quantifying effects of density on yields, which the reader would find a useful reference.

Application of reciprocal equations in intercropping

Despite the importance of intercropping (e.g. Willey, 1985; Ofori and Stern, 1987), only a few attempts have been made at exploring yield-density equations in intercropping (e.g. Wright, 1981; Park *et al.,* 2002). This has to do with the complexity of intercropping (Dolman, 1985; Tollenaar, 1992; Watkinson and Freckleton, 1997). As discussed previously given the peculiarities of intercropping, which involves two or more crop species, intra-specific competition has been distinguished from inter-specific competition (e.g. Firbank and Watkinson, 1985; Helenius and Jokinen, 1994). Accordingly, the reciprocal equations were modified to incorporate both inter-specific and intra-specific competition effects (Wright, 1981; Watkinson, 1981; Park *et al.,* 2002). In general, to improve yield advantage for intercropping the aim must be to reduce the effects of inter-specific competition as much as possible (Neumann *et al.,* 2009). Equations based on the inter-specific competitive effects approaches satisfactorily described data in some studies for the biomass and/or seed dry matter yields or both (Wright, 1981; Dolman, 1985; Baumann *et al.,* 2001; Park *et al.,* 2002; Neumann *et al.,* 2009). In some studies no attempts was made to separate the effects of intra-specific competition with the inter-specific competition (e.g. Bulson, 1991; Bulson *et al.,* 1997; Craufurd, 2000) because analyses were done using the usual approach for the sole crops based Equations 3 and 4 or other simple functions (e.g. linear, quadratic fits). This may be due to a limited range of densities of the two component crops involved. In other studies, the intra-specific and the inter-specific effects were separated (Shainsky, and Radosevich, 1992; Helenius and Jokinen, 1994; Watkinson and Freckleton, 1997; Park *et al.,* 2002; Neumann *et al.,* 2009).

Nevertheless, Wright (1981) can perhaps be credited as the one who first approached yield-density studies in intercropping with some novelty working with intercropped Italian rye grass (*Lolium multiflorum*)/ red clover (*Trifolium pratense*). His work was based on response surface design. This was because he varied both the total and individual densities systematically. Wright (1981) argued that given that Equation 4 determines the extent to which the density controls plant yield as the density was increased, if the 'competition function' of Holliday (1960a, b, c) holds, a logical extension of this equation for one component of an intercrop of crop types X and Y is given as follows

$$1/w_x = a_x + b_x p_x + c_{xy} p_y \qquad 12$$

And hence

$$Y_x = p_x \big/ \left(a_x + b_x p_x + c_{xy} p_y\right) \qquad 13$$

Where in Equations 12 and 13 the parameter a_x defines the factor that determines the genetic potential of a component X, while b_x defines the effects of increasing the density of X on yield of X. Similarly, p_x and p_y refers to the densities of the two intercrop components X and Y respectively, c_{xy} is a parameter that describes the effect of increasing density of plants of type Y on plant of type X.

In this equation, the term $b_x p_x$ causes a reduction in w_x as p_x increases corresponding to the reduction in weight per plant as the crop density increases (Dolman, 1985). The extra term $c_{xy} p_y$ in Wright's equation implies that an increase in density of a second component in the crop has similar effects on the weight per plant although this depends on the value of a_y compared with a_x. Thus, yield of the second component in the intercrop is described in similar fashion to the other component. Such that the following holds.

$$1/w_y = a_y + b_y p_y + c_{yx} p_x \qquad 14$$

And hence

$$Y_y = p_y \big/ \left(a_y + b_y p_y + c_{yx} p_x\right) \qquad 15$$

Where p_y is zero in Equations 12 and 13, the equations simplifies to sole crop of X, so that the parameters b_x and a_x are identical to b and a in the sole crop version (i.e. Equations 3 and 4). Thus, yields of the sole crop of X and Y tend towards $1/b_x$ and $1/b_y$ at high densities; while their yields as intercrop components tend towards $1/(b_x - c_{xy})$ and $1/(b_y - c_{yx})$ (Wright, 1981) provided that neither p_x nor p_y is very small. Baumann *et al.* (2001) applied the equation in celery (*Apium graveolens*)/leek (*Allium porrum*) intercropping and similar to Gooding *et al.* (2001), stated that a/b is the carrying capacity (which was different for the two crops in their research). Examples of some other investigations in which these equations were applied include those of Park *et al.* (2002) involving fodder maize (*Zea mays*)/Dwarf French bean (*Phaseolus vulgaris*) and Li and Watkinson (2000) involving carrot (*Daucus carota*)/*Chenopodium album*. Indeed, Watkinson and Freckleton (1997) applied a modified version of the equation to quantify the impact of *Arbuscular mycorrhiza* on plant competition.

Wright (1981) contended that both equations could be extended to allow for parabolic yield-density relationship in a similar way to the asymptotic equations by the introduction of the variate p^2_x, $p_x p_y$ and p^2_y. Similar approaches were described by Dolman (1985) even though the equations were deficient in quantifying yields in his investigations. According to them, the inter-specific parabolic equations for crop type X can be described as follows.

$$1/w_x = a_x + b_x p_x + c_{xy} p_y{}^2 \qquad 16$$

And hence

$$Y_x = \frac{p_x}{\left(a_x + b_x p_x + c_{xy} p_y{}^2\right)} \qquad 17$$

Similarly, the parabolic response of crop type Y in the intercrop can be described as follows

$$1/w_y = a_y + b_y p_{y_i} + c_{yx} p_x{}^2 \qquad 18$$

And hence

$$Y_y = \frac{p_y}{\left(a_y + b_y p_y + c_{yx} p_x{}^2\right)} \qquad 19$$

These parabolic inter-specific equations have rarely been applied in yield-density investigations. However, it should be stressed that Equations 16-19 are valid only when wide ranges of densities of the two components crops are involved, and the inter-specific asymptotic equations are deficient in quantifying yields satisfactorily. Indeed when wide range of densities of the two component crops are involved these equations are more efficient in describing parabolic yield-density relations than a simple intra-specific parabolic equation (i.e. Equations 5 and 6)

Dolman (1985) whose work was on intercropped carrot and onions (*Allium cepa*) and using a similar systematic design based on a response surface design as Wright, argued that it is necessary that an interactive term $d_{xy}p_xp_y$ and $d_{yx}p_yp_x$ is introduced to Equations 13 -15 such that the density of each component in the intercrop can have a different effect at different densities of the other component as described by Equations 20-23.

$$1/w_x = a_x + b_x p_x + c_{xy} p_y + d_{xy} p_x p_y \quad 20$$

And hence

$$Y_x = p_x \big/ \left(a_x + b_x p_x + c_{xy} p_y + d_{xy} p_x p_y\right) \quad 21$$

The yield of component Y can be quantified as follows

$$1/w_y = a_y + b_y p_y + c_{yx} p_x + d_{yx} p_y p_x \quad 22$$

And hence

$$Y_y = p_y \big/ \left(a_y + b_y p_{y_2} + c_{yx} p_x + d_{yx} p_y p_x\right) \quad 23$$

As was stated earlier, in Equations 20-23 the parameter a_x defines the factor that determines the genetic potential of component X, while b_x defines the effects of increasing the density of X on yield X. Similarly, p_x and p_y refers to the densities of the two intercrop components X and Y respectively, c_{xy} is a parameter that describes the effect of increasing density of plants of type Y on plant of type X. The parameter d_{xy} describes the effect of density of Y at each density of X on yield of X.

Dolman (1985) observed that the value of d_{xy} fitted to the carrot yields were negative, implying that the weight per plant could be affected by increasing the density of either carrot or onion. He asserted that the effect on the weight per carrot plant of a change in density of the onions was apparently about half that of the carrots. Again like Wright (1981), he tried fitting several equations to his data including the ones that have an additional quadratic term, which he concluded to be unnecessary because the asymptotic equations gave a better fit. Although, Dolman successfully applied his equations to describe yields of onion/carrot intercrop both of whom are of vegetative yields, to date the equations have not been applied to describe intercrops involving crops of reproductive yields. Therefore, it would be appropriate to evaluate the validity of these equations using crops of reproductive yields particularly at the same location. This is based on the premise that empirical models have greater validity in the areas they were developed (see Azam-Ali and Squire, 2002).

Establishing yield-density relationship using biologically meaningful equations have been shown to be an important preliminary requirement in the analyses of intercropping data (Dolman, 1985). For instance, Dolman (1985) applied asymptotic equations to evaluate intercrop consisting of crops of vegetative yield and used the fitted values in determining performance of intercropping based on land equivalent ratio (LER) estimates (see Willey, 1985). Where the yield responses were asymptotic, Dolman used the predicted asymptotic yield of the sole crop (i.e. $1/b_x$) as the divisor for standardization in determining intercrop efficiency. Hence, partial LER for crop type X (L_x) was calculated using Equation 24 to determine the LER based on fitted values.

$$L_X = \frac{XY_i}{\left(1/b_x\right)} \quad 24$$

Where XY_i refers to the fitted X intercrop yield and $1/b_x$ refers to the predicted asymptotic yield of the X sole crop.

Similar partial LER (L_y) calculations were done for the second component crop of the type Y as follows

$$L_y = \frac{YY_i}{\left(1/b_y\right)} \quad 25$$

Where YY_i refers to the fitted Y intercrop yield and $1/b_y$ refers to the predicted asymptotic yield of the Y sole crop.

Thus, the total intercrop LER (LER_{total}) was calculated simply as follows

$$LER_{total} = \left(\left(\frac{XY_i}{1/b_x}\right) + \left(\frac{YY_i}{1/b_y}\right)\right) \quad 26$$

Note that all parameters in Equation 26 are as defined in Equations 24 and/or 25 above.

Although this approach worked well in Dolman's research, this vital step in the analyses of results from intercropping research is rarely followed. The none application of this approach may be because the novel approach does not appear to be published by the author even though it is well documented in a higher degree thesis. Given that, Dolmans investigations involved crop of vegetative yields there is a need to apply this approach particularly for crops with reproductive yields.

Despite the novel approaches used by Wright (1981) and Dolman (1985), no attempt was done to explain the physiological basis responsible for the yield differences noticed as no measurement of resource use were carried out. Had these two investigations taken data on PAR and RUE for example, it is possible that cumulative PAR could have assumed similar asymptotic pattern as the biomass yields as was later shown by Gooding *et al.* (2002) for the wheat sole crop. Moreover, clearly their works were on vegetative yields. It has been demonstrated long ago that for crops with vegetative yields responses are asymptotic for the sole crops the crop provided they are well nourished and well managed (Willey and Heath, 1969; Bleasdale, 1966; 1967; 1984). More recently, it was suggested that the same yield-density relationship could hold for reproductive yield (e.g. Pinyosinwat, 2001; Salahi, 2002). Accordingly, it would be appropriate to apply the equations they have proposed to evaluate the productivity of intercrops in situations where yields are of reproductive types. Indeed, Helenius and Jokinen (1994) whose work was on oat (Avena sativa) /faba bean (*Vicia faba*) system, intercropped over a wide range of densities applied Equations 12 to 15 to quantify the biomass and seed dry matter yields in their studies but they did not use Equations 20 to 23 to ascertain whether they might be more appropriate.

Further notes on yield-density investigations in intercropping

Besides the works mentioned in the earlier sections of this paper, several authors including Watkinson (1981), Spitters (1983), Firbank and Watkinson (1985), Connolly (1987), Tollenaar (1992), Shainsky, and Radosevich (1992), Helenius and Jokinen (1994), Park *et al.* (2002) and Weigelt *et al.* (2007) just to mention a few have made substantial contribution in yield-density investigations and/or their application for agronomic purposes. For instance, Spitters (1983), stressed that it is possible to describe intra-specific stress (IS) for a given crop of the type X in an intercrop as follows

$$IS_x = \frac{b_x}{a_x} \qquad 27$$

Similarly, the IS for crop of the type Y in an intercrop can be described as

$$IS_y = \frac{b_y}{a_y} \qquad 28$$

In Equations 27 and 28 b_x, a_x, b_y and a_y are as defined in Equations 12 -15.

However, except the study of Helenius and Jokinen (1994), the index has not been widely used in yield-density investigations. The reciprocal equations assumed that it is possible to replace plants of the types Y with that of the type X in a certain ratio without changing weight per plant of X irrespective of the densities in which the exchange take place (Spitters, 1983; Helenius and Jokinen, 1994). Thus, the relative competitive ability (RCA) for component X can be described as follows

$$RCA_x = \frac{b_x}{c_{xy}} \qquad 29$$

Similarly, the RCA for component Y can be described thus

$$RCA_y = \frac{b_y}{c_{yx}} \qquad 30$$

In Equations 29 and 30 b_x, C_{xy}, b_y and C_{yx} are as defined in Equations 12 -15.

Although RCA values were determined for both oat and bean in the investigations of Helenius and Jokinen (1994), the index has not been widely used in yield-density investigations.

According to Connolly (1987), the substitution rate (S) provides a measure of equivalence between the two components in an intercrop. The S for crop of the type X can be described thus

$$S_x = \frac{c_{xy}}{b_x} \qquad 31$$

Similarly, the S for crop of the type Y is given as follows

$$S_y = \frac{c_{yx}}{b_y} \qquad 32$$

In Equations 31 and 32, C_{xy}, b_x, C_{yx} and b_y are as defined in Equations 12 -15.

The investigations by Helenius and Jokinen (1994) indicate that for the seed yield S were 0.33 and 0.72 for oat and bean respectively. This suggests that oat had greater effects on beans than beans had on oat. In other words, for the seed yield their research indicates that oat was the dominant component and beans the suppressed or dominated component. Similar to the earlier indices, except the study of Helenius and Jokinen (1994), the index has not been widely used in yield-density investigations. However, S appears to have similar interpretation with the equivalent coefficient index Park *et al.* (2002) more recently applied in their investigations.

Spitters (1983) proposed the niche differentiation indexes (NDI) to rank the relative strength of intra-specific competition and the inter-specific competition. According to Helenius and Jokinen, (1994) the double ratio NDI helps in analysing the partitioning of resources. In situations where the double ratio value is greater than 1 the yield advantage of the given intercrop can be attributed to differences in resource requirement (e.g. soil nitrogen) by the two component crops. Based on Equations 12 and 13, NDI for crop of the type X and Y can be described thus

$$NDI = \left(\frac{\left(b_x / c_{xy} \right)}{\left(b_y / c_{yx} \right)} \right) \qquad 33$$

In Equations 33 C_{xy}, b_x, C_{yx} and b_y are as defined in Equations 12 -15.

The investigations by Helenius and Jokinen (1994) indicate that NDI were 4.46 and 4.10 for biomass and seed yield respectively. They attributed yield advantage to differences in soil nitrogen captured by oat and bean component crops. Baumann *et al.* (2001) also calculated NDI for the total biomass in celery/leek intercropping system with values of 0.95 and 0.97 for the 1995 and 1996 experiments respectively. This indicates lack of differential resource requirement between the two crops in an intercrop. Recently, Neumann *et al.* (2009) also calculated NDI for intercrops of pea and oat achieving values of 18.00 and 10.6 for the 2002 and 2003 experiments respectively. This clearly indicates higher degree of resource complementarity between the two crops in an intercrop. As Neumann *et al.* (2009) suggested due attention needs to be given to the calculation of NDI in yield-density investigations given that the index does not appear to be widely adopted. Indeed, this index may be of particular relevance in yield-density investigations in which no data on resource use was taken. For instance provided water and nutrients were not limiting, it can be easily concluded that positive NDI values may be due to differential utilization of PAR and RUE by the two component crops.

Wright (1981) proposed the potential yield advantage (PYA) or the potential productivity of an intercrop. Where the value of PYA exceeds b_x and b_y for example in the equations he proposed (i.e. Equation 12 -15), the intercrop will outyield both components grown in sole crop.

The potential yield advantage for crop of types X and Y in an intercrop can be described as

$$PYA = \left(C_{xy} \times C_{yx}\right)^{1/2} \qquad 34$$

In Equation 34, C_{xy}, and , C_{yx} are as defined in Equations 12 -15. Interestingly, this is a different approach at measuring the productivity of an intercrop from the widely used method of LER (e.g. Willey, 1984), involving two crop combinations grown in wide densities each. Nevertheless, except the investigations of Helenius and Jokinen (1994), others in yield-density investigations or in intercropping research in general have rarely applied this approach.

Recommendations for future research

The foregoing shows that more recently some research has been carried out on yield-density relations in sole cropping and intercropping particularly with temperate crops. It appears density investigations and density combinations trials using tropical crop species appear to be restricted in most case to the traditional ANOVA procedures alone despite its limitation. This paper advocates for the application of competitive approach to analysing density trials irrespective of the crop species involved and/or location of the investigation, as is represented by the application of yield-density equations.

It should be emphasised that despite the increasing attention given to intercropping research, there has been little attention to explore yield-density equations particularly for crops of reproductive yields. The simple asymptotic and parabolic equations appear to be increasingly applied in agronomic investigations particularly for the sole crops. However, the derivatives of these simple intra-specific equations (e.g. Counce, 1987; Ellis *et al.*, 1999) appear to have been less applied by researchers. Although Counce (1987) suggested that Equation 7 can describe optimum yields well if response to density were asymptotic under sole cropping conditions. For intercropping there may be a need to modify this equation particularly in investigations were wide density of the two component crops are involved, as with the response surface design, for example.

Similarly, of lesser applicability in agronomic research are the inter-specific yield-density equations (both the asymptotic and parabolic types). Indeed, only a few intercropping experiments applied the inter-specific equations (see Wright, 1981; Watkinson, 1981; Helenius and Jokinen, 1994). The modified inter-specific equation (e.g Dolman, 1985) has not been applied either for any crop combinations. These inter-specific yield-density equations would find particular relevance in intercropping research involving wide densities of the two component crops. However, it is worth mentioning that most of these inter-specific equations assumed equal competitive ability between the components crops (Wright 1981), hence are deficient in describing satisfactorily a simple additive intercrop. It is clear that the competitive ability of the two component crops may not be equal in such cases. Consequently, the assumptions of several equations reviewed (e.g. Wright, 1981; Dolman, 1985) may not hold true.

Thus, it appears there may be a need to explore yield-density equations as it relates to a simple additive intercrop more deeply. It is speculated that the total intercrop yield as well as the yield of the major component can be described using a simpler asymptotic and/or parabolic equation with the minor component quantified as the difference between the two. Yield-density responses in replacement intercrops are a huge subject of its own but have been well investigated (e.g. Neumann *et al.*, 2009) so were not discussed in this paper. Nevertheless, it should be reiterated that irrespective of the design involved, if the benefit of intercropping is to be realized, the aim must be to reduce inter-specific competition relative to intra-specific competition. This indicates that there may be need to evaluate the performance of intercropping compare to the sole crops after establishing yield-density relationship following some of the methods described earlier (e.g. Dolman, 1985). Indeed, the application of some of the competitive indices (e.g. Spitters, 1983) and methods of estimating intercrop performance (e.g. Dolman, 1985) in understanding results from yield-density investigations is worthy and needs to be given due attention.

Conclusions

This paper clearly indicates that substantial progress has been done more recently on yield-density relationships investigations. However, whilst the intra-specific yield-density equations are increasingly been applied to quantify seed yields, biomass yields and in some cases PAR, the inter-specific equations have not received wider application especially with regards to crops of reproductive yields. Indeed, despite the widespread practice of intercropping in different regions of the world, limited attention has been paid to quantify yields using the competitive approach reviewed in this paper. This paper concludes that the analyses of density trials for both sole crops and intercrops may be more meaningful when some of the equations and their derivatives reviewed here are applied to quantify yields.

References

Azam-Ali SN, Squire GR. 2002. Principles of Tropical Agronomy. Wallingford, UK: CABI.

Azam-Ali SN, Nageswara RC, Craigon J, Wadia KDR, Williams JH. 1993. A method for calculating the population/yield relations of groundnut (*Arachis hypogeae*) in semi-arid climates. Journal of Agricultural Sciences **121**, 213-222.

Baumann DT, Bastiaans L, Kropff MJ. 2001. Competition and crop performance in a leek-celery intercropping system. Crop Science **41,** 764-774.

Bleasdale JKA. 1966a. Plant growth and crop yield. Annals of Applied Biology **57,** 173-182.

Bleasdale JKA. 1966b. The effects of plant spacing on the yield of bulb onions (*Allium cepa* L.) grown from seed. Journal of Horticultural Science **41,** 145-153.

Bleasdale JKA. 1967. The relationship between the weight of a plant part and total weight as affected by plant density. Journal of Horticultural Science **42**, 51-58.

Bleasdale JKA. 1984. Plant Physiology in Relation to Horticulture, 2nd edition. London: MacMillan.

Bleasdale JKA, Nelder JA. 1960. Plant population and crop yield. Nature **188,** 342.

Bulson HAJ. 1991. Intercropping wheat with field beans in organic farming systems. PhD Thesis, University of Reading, United Kingdom.

Bulson HAJ, Snaydon RN, Stopes CE. 1997. Effects of plant density on intercropped wheat and field beans in an organic farming system. Journal of Agricultural Sciences **128,** 59-71.

Connolly J. 1987. On the use of response models in mixture experiments. Oecologia **72**, 95-103.

Counce PA. 1987. Asymptotic and parabolic yield and linear nutrient content responses to rice population density. Agronomy Journal **79,** 864-869.

Craufurd PQ. 1996. Effects of plant population density on dry matter partitioning and yield in a short-duration cultivar of cowpea (*Vigna unguiculata*) grown in the tropics. Journal of Agricultural Science **127**, 89-96.

Craufurd PQ. 2000. Effect of plant density on the yield of sorghum-cowpea and pearl millet-cowpea intercrops in northern Nigeria. Experimental Agriculture **36,** 379-395.

Dolman G. 1985. Density trials with systematic designs on intercropped carrots and onions. PhD Thesis, University of Reading, United Kingdom.

Ellis RH, Salahi M. 1997. Optimizing inputs for contrasting cultivars: Quantifying the effects of plant population density and nitrogen fertilizer on the yield of four cultivars of spring wheat. Aspects of Applied Biology **50,** 139-146.

Ellis RH, Salahi M, Jones SA. 1999. Yield-density equations can be extended to quantify the effect of applied nitrogen and cultivar on wheat grain yield. Annals of Applied Biology **134**, 347-352.

Farazdaghi H, Harris PM. 1968. Plant competition and crop yield. Nature **217,** 289-290.

Firbank LG, Watkinson AR. 1985. On the analysis of competition within two-species mixtures of plants. Journal of Applied Ecology **22,** 503–517.

Francis CA. 1989. Biological efficiencies in multiple-cropping systems. Advances in Agronomy **42**, 1-42.

Fukai S, Trenbath BR. 1993. Processes determining intercrop productivity and yields of component crops. Field Crops Research **34**, 247-271.

Giunta F, Pruneddu G, Motzo R. 2009. Radiation interception, biomass and nitrogen accumulation in different cereal and grain legume species. Field Crops Research **110,** 76-84.

Gooding MJ., Pinyosinwat A, Ellis RH. 2001. The response of wheat grain nitrogen concentration to plant population density. Aspects of Applied Biology **64,** 157-162.

Gooding MJ, Pinyosinwat A, Ellis RH. 2002. Responses of wheat grain yield and quality to seed rate. Journal of Agricultural Science **138,** 317-331.

Heath SB. 1970. An examination of the biological significance, which can be attributed to the quantitative relationships between plant population and crop yield. PhD Thesis, University of Reading, United Kingdom.

Helenius J, Jokinen K. 1994. Yield advantage and competition in intercropped oats (*Avena sativa* L.) and faba bean (*Vicia faba* L.): application of the hyperbolic yield-density model. Field Crops Research **37,** 85-94.

Holliday R. 1960a. Plant population and crop yield: part I: Field Crop Abstracts **13**, 159-167.

Holliday R. 1960b. Plant population and crop yield: part II: yield and plant population in British crops. Field Crop Abstract **13**, 247-254.

Holliday R. 1960c. Plant population and crop yield. Nature **186**, 22-24.

Innis D. 1997. Intercropping and the scientific basis of traditional agriculture. London, UK: Intermediate Technology publication.

Khah EM, Roberts EH, Ellis RH. 1989. Effect of seed ageing on growth and yield of spring wheat at different plant-population densities. Field Crops Research **20**, 175-190.

Kindred DR, Gooding MJ. 2005. Heterosis for yield and its physiological determinants in wheat. Euphytica **142,** 149-159.

Law R, Watkinson AR. 1987. Response-surface analysis of two species competition: An experiment on *Phleum arenarium* and *Vulpia fasciculata*. The Journal of Ecology **75,** 871-886.

Li B, Watkinson AR. 2000. Competition along a nutrient gradient: A case study with *Daucus carota* and *Chenopodium album*. Ecological Research, **15,** 293-306.

Mead R. 1970. Plant density and crop yield. Applied Statistics **19**, 64-81.

Mead R. 1979. Competition experiments. Biometrics **35,** 41-54.

Mligo JK, Craufurd PQ. 2007. Productivity and optimum plant density of pigeonpea in different environment in Tanzania. Journal of Agricultural Science **145,** 343-351.

Neumann A, Werner J, Rauber R. 2009. Evaluation of yield-density relationships and optimization of intercrop compositions of field grown pea-oat intercrops using the replacement series and the response surface design. Field Crops Research **114,** 286-294.

Ofori F, Stern WR. 1987. Cereal-legume intercropping systems. Advances in Agronomy **41,** 41-90.

Park SE, Benjamin LR, Watkinson AR. 2002. Comparing biological productivity in cropping systems: A competition approach. The Journal of Applied Ecology **39,** 416-426.

Pinyosinwat A. 2001. The effect of seed rate on the yield and quality of wheat and its interaction with other agronomy practices. PhD Thesis, University of Reading, United Kingdom.

Rejmanek M, Robinson GR, Rejmankova E. 1989. Weed-crop competition: experimental designs and models for data analysis. Weed Science **37,** 276-284.

Salahi MM. 2002. Yield and quality of cereals in response to input and spatial variability. PhD Thesis, University of Reading, United Kingdom.

Shainsky LJ, Radosevich SR. 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. Ecology **73,** 30-45.

Shinozaki K, Kira T. 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. Journal of the Institute Polytechnic Osaka City , University Series **D7,** 35-72.

Shirtliffe SJ, Johnston AM. 2002. Yield-density relationships and optimum plant populations in two cultivars of solid-seeded dry bean (*Phaseolus vulgaris* L.) grown in Saskatchewan . Canadian Journal of Plant Science **82**, 521-529.

Spitters CJT. 1983. An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. Netherlands Journal of Agricultural Science **31,** 1-11.

Tollenaar H. 1992. Reinterpretation and evaluation of some simple descriptive models for weed-crop interference in terms of one-sided and two-sided competition. Oikos **65,** 256-264.

Vandermeer J. 1989. The Ecology of intercropping. Cambridge, UK: Cambridge University press.

Watkinson AR. 1981. Interference in pure and mixed populations of Agrostemma githago . Journal of Applied Ecology **18,** 967-976.

Watkinson AR, Freckleton RP. 1997. Quantifying the impact of *arbuscular mycorrhiza* on plant competition. Journal of Ecology **85,** 541–545.

Weigelt A, Schumacher J, Walther T, Bartelheimer M, Steinlein T, Beyschlag W. 2007. Identifying mechanisms of competition in multi-species communities. Journal of Ecology **95,** 53-64.

Willey RW. 1985. Evaluation and presentation of intercropping advantages Experimental Agriculture **21**, 119-133.

Willey RW, Heath SB. 1969. The quantitative relationship between plant population and crop yield. Advances in Agronomy **21**, 281-321.

Wright AJ. 1981. The analysis of yield-density relationship in binary mixtures using inverse polynomials. Journal of Agricultural Science **96,** 561-567.