The Quantitative Relationships between Plant Population and Crop Yield

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I. Introduction

It may often be desirable for the agronomist to define the relationships between plant population and crop yield quantitatively. Probably the simplest reason for wishing to do this is to evaluate such characteristics as optimum population and maximum yield. This can be a useful end in itself, and it can also facilitate comparisons between different cropping situations. The latter aspect is particularly useful when the factors being examined interact with population, for comparisons can clearly be misleading if they are not made between comparable points on the population response curve. Putter et al. (1966) have pointed out that even comparisons between calculated parameters which have little or no biological meaning can be of value, for these may still help to pinpoint essential differences.

It is more usual, however, that the agronomist wishes to define the relationships between plant population and crop yield so that in any future situation he can predict yield/population curves easily and accurately from the minimum of data. For this purpose at least, it is desirable that an equation defining these relationships should not be

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merely a mathematical empiricism but should be so far as possible an accurate description of the biological processes of competition that are involved. Some biological validity of this nature clearly provides greater justification for the use of an equation and at the same time probably ensures a wider applicability. However, any attempt to derive such an equation inevitably involves some degree of compromise, for the very nature of the problem is to describe extremely complex biological processes by a mathematical function sufficiently simple to be of use to an agronomist. The object of this review is to examine some of these equations and to discuss how far they fulfill the agronomist's needs. But first some general points must be discussed.

It is important to realize that plant population should be defined not only in terms of the number of plants per unit area (i.e., *plant density*) but also in terms of the arrangement of these plants on the ground (*spatial arrangement* or *plant rectangularity*). Few workers have distinguished between these two factors and many plant population experiments have in effect studied the combined effects of both; this is certainly the case where different populations have been studied at a constant row width. Since most workers seem to have assumed that the only effect of population is one of density, it would seem logical to try to define the relationship between crop yield and density first, and to incorporate the effects of rectangularity subsequently. For this reason, the rectangularity factor is ignored when the equations in Section II are discussed, even though this factor has not been eliminated in many of the experiments that will be quoted. A possible means of incorporating the rectangularity factor into an equation is discussed in Section III.

Crop yield itself may also require further definition, for in some crops the grower is as much concerned with the yield of the individual plant as with yield per unit area. Many population experiments have examined yield per plant, but it has almost invariably been in terms of *mean yield* per plant. Yet the degree of variation in yield of the individual plants within a factor that can determine the total yield of plants within a given size grading. Some studies in which an attempt has been made to estimate this variation are briefly discussed in Section IV.

Finally, it is pertinent to point out that it is not always easy to decide upon the correct unit of plant population. This was emphasized by Holliday (1960b), who suggested that it should be the basic *independent* plant unit, whether this was a tiller in a grass crop or perhaps an individual stem in a potato crop. Accurate identification of these population units could be of particular importance in quantitative studies, for without this it may be even more difficult to produce reliable and meaningful equations applicable to a wide range of crops.

II. Relationships between Plant Density and Crop Yield

A. BIOLOGICAL RELATIONSHIPS

Before examining the different yield/density equations, it is first necessary to decide what are the basic biological relationships that these equations are attempting to describe. The only real attempt to classify these relationships seems to have been that of Holliday (1960b). He suggested that there were essentially two relationships: an *asymptotic* one where, with increase in density, yield rises to a maximum and is then relatively constant at high densities; and a *parabolic* one where yield rises to a maximum but then declines at high densities. For the purposes of this present review this suggested classification is a useful one to adopt, but no exact mathematical description is inferred by the terms asymptotic and parabolic.

It may well be argued, of course, that these two suggested relationships are merely different degrees of expression of a single relationship. However, in the present context the important fact to realize is that the two situations exist, for it may often happen that a given yield/density equation can describe either an asymptotic situation or a parabolic situation, but not both. Also, since the mathematical description of these two situations can be quite different, it is mathematically convenient to separate them.

It is not within the scope of this review to discuss in detail which specific crops or types of yield may conform to the different biological relationships; nor is it possible to consider how these relationships may be affected by the level of supply of different growth factors. At the same time it may be of use to give an indication of some of the cropping situations in which the different relationships can occur and to illustrate the shapes of yield/density curves which need description.*

1. The Asymptotic Relationship

Holliday (1960b) suggested that total crop dry matter conformed to this relationship, but more recently several workers (de Wit, 1959; Bleasdale, 1966a; Bruinsma, 1966; Campbell and Viets, 1967; Farazdaghi, 1968) have shown that at high densities dry matter decreases in this form of yield can occur. Despite these exceptions it is probably reasonable to assume that, for practical purposes, total dry matter yield often conforms to an essentially asymptotic relationship. This situation is illustrated in

*The notation used to express the relationships is as follows: y = yield per unit area; ρ = plant density; s = space available per plant ($s = 1/\rho$); d_r = distance between plants within a row (intrarow spacing); d_s = distance between rows (interrow spacing); w = yield per plant; W = maximum yield attainable by a plant; w_p = yield of a plant part. Any variable or constant with the subscript p, as in w_p above, refers to a plant part as opposed to a total plant.

Figs. 1A and 1B by some data for fodder rape (Holliday, 1960a) and for Wimmera ryegrass and subterranean clover (Donald, 1951), all of which are asymptotic to particularly high densities.

Holliday (1960b) also suggested that those forms of yield which constituted a vegetative part of the crop conformed to an asymptotic relationship. Notable exceptions may occur (see Section II,A,2) but again it is reasonable to assume that such forms of yield often are asymptotic. This situation is illustrated by some data for potato tubers (Saunt, 1960) and root yield of long beet (Warne, 1951) in Figs. 1C and 1D, respectively.

2. The Parabolic Relationship

Holliday (1960b) suggested that reproductive forms of yield (i.e., grains and seeds) conformed to a parabolic relationship, and the examples
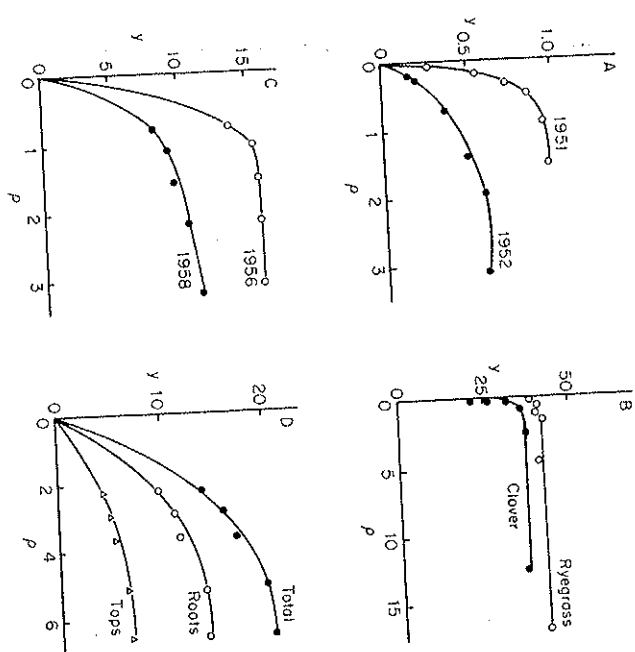

FIG. 1. Examples of the asymptotic yield/density relationship. (A) Total dry matter of Essex Giant rape: y = tons/acre, $\rho = 10^6$ plants/acre (Holliday, 1960a). (B) Total dry matter of Wimmera ryegrass and subterranean clover: y = g./sq. lk., $\rho = 10^2$ plants/sq. lk. (Donald, 1951). (C) Fresh weight of potato tubers: y = tons/acre, $\rho = 10^4$ parent tubers/acre (Saunt, 1960). (D) Fresh weight yields of long beet: y = pounds/plot, $\rho = 10^4$ plants/foot of row (Warne, 1951).

given in Figs. 2A and 2B for grain yield of maize (Lang et al., 1956) and barley (Willey, 1965) certainly indicate that this can be so. The maize data are of particular interest because this crop usually displays a very distinct decline in yield at high densities, and as such it represents one of the more extreme forms of the parabolic relationship. The barley data, in which the density reaches a particularly high value, are also of interest because they illustrate a point seldom evident in experimental data,
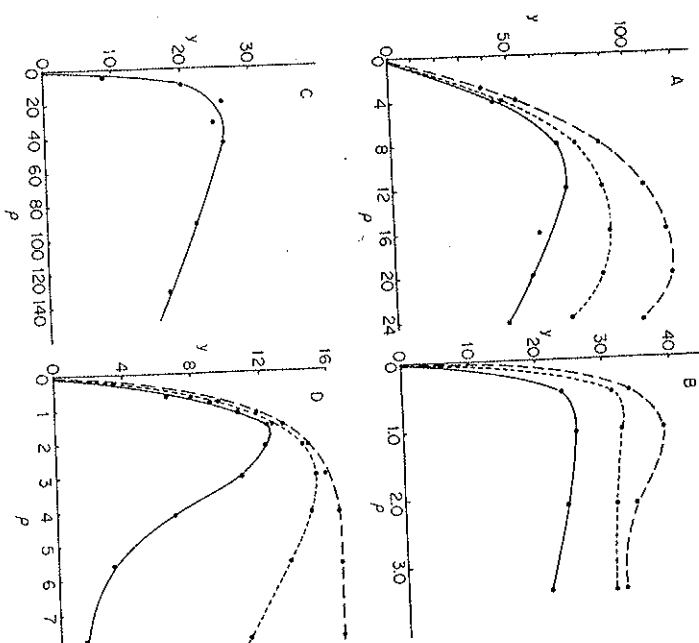

FIG. 2. Examples of the parabolic yield/density relationships. (A) Mean grain yield of maize for all hybrids, grown at a low level (——), medium level (——), and a high level (— — —) of nitrogen: y = bushels/acre, $\rho = 10^3$ plants/acre (Lang et al., 1956). (B) Grain yield of barley grown with 0 (——), 30 (——), and 60 (— — —) units of nitrogen: y = cwt/acre, $\rho = 10^6$ plants/acre (Willey, 1965). (C) Root dry weight of globe red beet: $y = 10^2$ kg./acre, $\rho = 10^4$ plants/acre (unpublished Reading data). (D) Parsnips var. AVONRESISTOR, total fresh weight yield (— — —), graded yield > 1.5 inches in diameter (——), graded yield > 2.0 inches in diameter (——): y = tons/acre, ρ = plants/sq. ft. (Bleasdale and Thompson, 1966).

namely that the parabolic relationship must at some stage begin to flatten off along the density axis. As mentioned in Section II,A,1, certain forms of vegetative yield may also be parabolic. A notable instance of this seems to be the root yield of globe red beet, and some example data for this crop are given in Fig. 2C.

Yet a further situation can exist where yield is parabolic, and this is where yield constitutes only those plants, or parts of plants, that fall within certain size limits, i.e., where some form of "grading" is practiced. Figure 2D illustrates this situation with some parsnip data of Bleasdale and Thompson (1966). It can be seen that in this particular instance total yield of roots is asymptotic, but grading produces a parabolic relationship that becomes more acute as the severity of grading is increased. This situation is of considerable importance in many crops. However, it must be emphasized that "graded" yield cannot be regarded as a biological form of yield in the same sense as those forms discussed above. For this reason, the description of this particular relationship may have to remain more empirical than that of other relationships.

B. YIELD/DENSITY EQUATIONS

Section II,A indicated the general form of the biological relationships that exist between crop yield and plant density. The object of this section is to describe the different mathematical equations that have been proposed to define these relationships. Some of these yield/density equations propose a relatively simple mathematical relationship directly between yield per unit area and density, but the majority propose a basic relationship between mean yield per plant and density. The general shape of this latter relationship is illustrated in Fig. 3 for both the asymptotic and parabolic yield/density situations.

1. Polynomial Equations

One of the simplest approaches to the description of yield/density relationships has been the use of two polynomial equations applied directly to the relationship between yield per unit area and density. These have been used largely as a convenient means of smoothing experimental data: they have not been seriously proposed as general yield/density equations, and little or no biological validity has been claimed for them. In these respects they are not of any major importance in the present review, but a brief description of their scope and limitations serves as a useful introduction to the use of yield/density equations, particularly where biological validity is lacking.
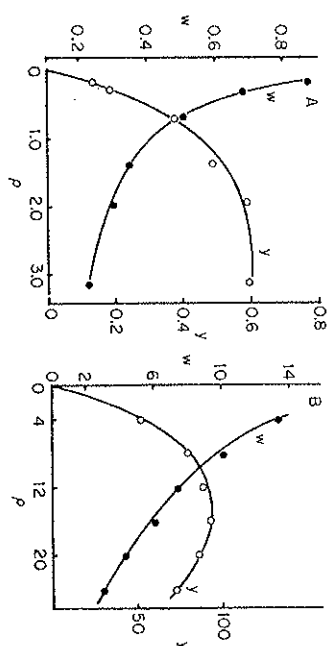
Hudson (1941) attempted to describe the relationship between grain yield and seed rate of winter wheat with a simple quadratic expression:

$$y = a + b\rho + c\rho^2 \tag{1}$$

where a, b, and c are constants, c being negative. The general shape of the yield/density curve described by Eq. (1) is illustrated in Fig. 4, where

Fig. 3. The relationship between yield per plant (w) and plant population (ρ) in an asymptotic (A) and a parabolic (B) yield/density situation. (A) Total dry matter of Essex Giant rape, 1952 experiment; y = tons/acre, $w = 10^{-6}$ ton/plant, $\rho = 10^6$ plants/acre (Holliday, 1960a). (B) Grain yield of maize hybrid WF9 × 38-11 at medium N; y = bushels/acre, $w = 10^{-3}$ bushel/plant, $\rho = 10^3$ plants/acre (Lang et al., 1956).
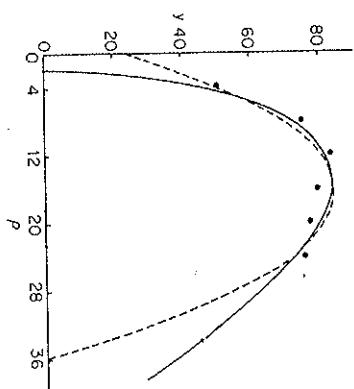
Fig. 4. The quadratic equation (Eq. 1) (——) and the square root equation (Eq. 2) (———) fitted to grain yield of maize hybrid HY2 × OH7 at low N; y = bushels/acre, $\rho = 10^3$ plants/acre (Lang et al., 1956).

it is fitted to some maize data of Lang et al. (1956); it is essentially a curve which is symmetrical about a maximum value of yield. Although the degree of curvature may obviously vary, this basic shape offers little flexibility in fitting yield/density relationships. It is clearly not suitable for fitting a truly asymptotic situation, and in a parabolic situation it is likely to give a good fit only where the yield/density curve is reasonably symmetrical. But even in this latter situation, the accuracy of this equation is probably restricted to a relatively narrow range of densities around the point of maximum yield. This is because of the unrealistic implications of the equation at both high and low densities. At high densities it implies that yield must drop sharply down to zero (see extrapolation in Fig. 4), whereas at the other extreme it implies that at zero density yield has a value, a (which in practice may turn out to be either positive or negative). The former implication is a serious limitation on the use of this equation at high densities. The latter implication could be only a minor disadvantage if the value of a was low; in any case, if an accurate fit at low densities was particularly desirable, the omission of a from the equation would ensure that the curve passed through the origin.

The disadvantage of the symmetrical nature of the quadratic curve was avoided by Sharpe and Dent (1968) by using a square root form of polynomial (Eq. 2):

$$y = a + b\rho + c\sqrt{\rho} \qquad (2)$$

where a, b, and c are constants, b being negative. This equation again gives rise to a curve where yield rises to a maximum value and then decreases at higher densities, so it still cannot describe an asymptotic situation. Compared with the quadratic, however, it can follow a slightly more gradual decline in yield at high densities, although this is accompanied by a rather steeper increase at the low densities (see Fig. 4). It still implies that at zero density yield has a finite value a, and that at the other end of the scale yield declines to zero, although admittedly at a rather higher density than with the quadratic.

The apparent lack of any biological validity must also impose limits on the use of these two equations. For example, it would seem unwise to use them where data were not sufficiently comprehensive to give a good initial indication of the general shape of any particular yield/density situation. Also there would seem little justification for using them to extrapolate data. Such extrapolation was carried out by Keller and Li (1949), who used the quadratic to estimate optimum density and maximum yield of some hop data, and it is of significance that when Wilcox (1950), with

little more justification, extrapolated the same data using the Mitscherlich equation he obtained substantially different values.

2. Exponential Equations

Duncan (1958), when reviewing experimental data on maize, proposed an exponential equation to describe the relationship between grain yield and density. He derived this by fitting a linear regression of the logarithm of yield per plant on density. The basic relationship was therefore:

$$\log w = \log K + b\rho \qquad (3)$$

or

$$y = \rho \, K \, 10^{b\rho}$$

comment that $\int \frac{1}{w} dw = \ln w$

where K is a constant and b, negative, is the slope of the regression line (see Fig. 5A). Carmer and Jackobs (1965) used this equation in a slightly different but analogous form:

$$y = \rho \, A \, K^{\rho}$$

where A and K are constants. The yield/density curve which this type of equation produces is comparable to the polynomials in as much as yield must rise to a maximum value and then decrease at higher densities. It can give a good fit to parabolic yield/density data, but even though it is much more flexible than the polynomials at high densities, it still cannot
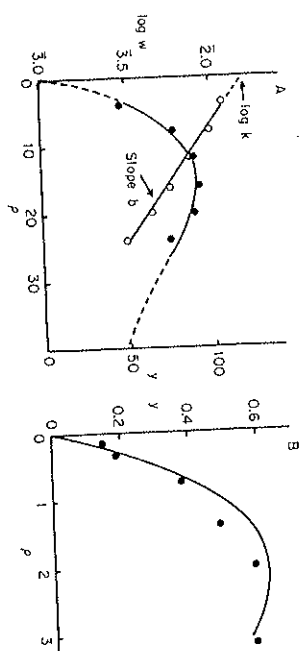
FIG. 5. The exponential equation (Eq. 3) of Duncan (1958) fitted to a parabolic (A) and an asymptotic (B) yield/density relationship. (A) The regression line of log w against ρ, and the fitted yield/density curve for grain yield of maize, mean of all hybrids at medium N; y = bushels/acre, ρ = 10³ plants/acre, w = 10⁻³ bushel (Lang et al., 1956). (B) The fitted yield/density curve for total dry matter of Essex Giant rape, 1952 data; y = tons/acre, ρ = 10⁶ plants/acre (Holliday, 1960a).

give a useful practical fit to data that are asymptotic. This is illustrated in Fig. 5, where it is fitted to some parabolic maize data of Holliday (1960a) and some asymptotic rape data of Lang *et al.* (1956)

Apart from greater flexibility, this exponential equation has further advantages over the polynomials. At high densities the yield curve does not cut the density axis but, more realistically, only gradually approaches it. Also, this curve now passes through the origin. However, as pointed out by Duncan there may still be a defect at low densities for, as extrapolation of the regression line in Fig. 5A indicates, the equation cannot allow for a leveling off in yield per plant at densities too low for competition to occur. But this is a common defect of yield/density equations, and it is discussed later when considering Holliday's reciprocal equations (Section II,B,5,b).

Duncan also pointed out that, since his equation was based on a linear regression, it was possible to construct the whole yield/density curve from the yields at only two densities. He therefore suggested that in the maize crop the examination of factors that interacted with density might usefully be carried out at two densities; the use of his equation would then allow comparison of the factors at their calculated points of optimum density and maximum yield. This technique can, of course, be used with any yield/density equation derived from some linear regression on density, and its practical potential makes it of considerable interest. Its application calls for some caution, however, for a prerequisite for its use must be a reasonable assurance that the equation used is an accurate description of the particular yield/density relationship that is under study. Duncan's justification for suggesting its use in the maize crop was the fact that his equation gave a good practical fit to the data he reviewed. This seems reasonable, but in general a better justification would seem to be the knowledge that an equation used in this way had a good deal of biological validity and was not just an empirical one. This could be particularly important, because it was pointed out by Duncan that the farther apart the two densities, the more accurately the regression line would be determined. While this may be mathematically sound, it would seem safer in practice to include a third intermediate density so that the point of calculated maximum yield is not too far from an experimental treatment.

3. Mitscherlich Equation

Mitscherlich proposed a law of physiological relations by which he described the relationship between the yield of a plant and the supply of an essential growth factor, all other factors being held constant. He assumed that as the supply of such a factor increased, yield per plant

would approach a maximum value, and at any given point the response would depend on how far the plant yield was below this maximum. This can be expressed:

$$\frac{dw}{df} = (W - w)c$$

where *f* is the level of supply of the factor and *c* is a constant. On integration this gives Eq. (4):

$$w = W (1 - e^{-cf}) \tag{4}$$

Mitscherlich termed *c* his "Wirkungsfactor" and claimed that it was constant for a given growth factor and independent of other conditions. Later, Mitscherlich (1919) suggested that his equation might be applied more generally to the relationship between "space" and plant growth and so serve as a yield/density equation. Thus, substituting space, *s*, for the growth factor, *f*, Eq. (4) can be rewritten:

$$w = W (1 - e^{-ks}) \tag{5}$$

where *K* is now a general "space" constant or factor. It is evident from the basic assumption about the nature of the plant's response that this yield/density equation describes an asymptotic situation but not a parabolic one.

Kira *et al.* (1954) examined the constancy of the space factor *K*. Using the yield/density data of Donald (1951) for subterranean clover, they were able to define the asymptotic value of yield per plant, *W*. From this value, and from mean yields per plant at the other densities, they calculated a range of *K* values (Table I). It is apparent that the values decreased with increase in the space available per plant and could not be regarded as constant. Kira *et al.* (1954) obtained similar changes in *K* values from yield/density data for azuki bean (*Phaseolus chrysanthus*), although the trend was not so clear.

This change in the value of *K* could have interesting agronomic implications, for it may perhaps suggest that a change in density may not only change the space available to a plant, but might also bring about some change in the environment—for example, an effect on rooting depth. However, as far as the practical use of the Mitscherlich equation is concerned, a change in *K* is clearly undesirable, and the value of this expression as a yield/density equation becomes questionable. Kira *et al.* (1954)

TABLE I

MITSCHERLICH'S FORMULA APPLIED TO THE RESULTS OF AN EXPERIMENT WITH SUBTERRANEAN CLOVER OF DONALD (1951)[a]

Density (plants/sq. link)	61 days from sowing		131 days from sowing		182 days from sowing	
	Dry weight per plant (g.)	K	Dry weight per plant (g.)	K	Dry weight per plant (g.)	K
0.25	15.6	—	528	—	34,080 (W)	0.00020
1.00	15.5	—	562 (W)	—	21,280	0.00061
5.95–5.93	15.6	—	386	0.0073	4,560	0.00091
15.9–16.13	15.8 (W)	—	364	0.0178	2,020	0.00106
60.6–62.6	14.2	0.154	153	0.0213	600	0.00117
241–248	13.9	0.563	73	0.0370	160	0.00125
1247–1393	10.6	1.66	16	0.0430	29	0.00123

[a] After Kira et al. (1954).

did in fact point out that they could stabilize K by arbitrarily reducing the value of W, but in this event the equation must lose much of its biological foundation.

Despite these criticisms of the Mitscherlich equation, the basic concept of an asymptotic yield per plant is of considerable interest. This at least provides a satisfactory theoretical description of the yield/density curve at very low densities where there is no competition. As several workers have pointed out (Duncan, 1958; Kira et al., 1954; Shinozaki and Kira, 1956; Holliday, 1960a), yield/density curves are usually unable to provide such a description and their validity at low densities is doubtful. It is also of interest that Goodall (1960), examining some mangold data, and Nelder (1963), commenting on some lucerne data of Jarvis (1962), both found that the Mitscherlich equation could give as good a fit as other equations. On the other hand, as would be expected from the results of the examination of his K values by Kira et al. (1954), Donald (1951) did not obtain a good fit to his data using the Mitscherlich equation.

4. Geometric Equations

Geometric equations were put forward by Warne (1951) and Kira et al. (1953) to describe certain yield/density relationships; the latter workers used the term "power" equation. Essentially this type of equation assumes a linear relationship between the logarithm of yield per plant and the logarithm of density.

Warne (1951) was studying the effect of density on the yield of root vegetables (beet, parsnips, and carrots), and he proposed a linear relationship between the logarithm of root yield per plant and the logarithm of distance between plants in the row where row width was constant. Since the row width was constant Warne's equation can be written in the form

$$\log w = \log A + b \log (s) \qquad (6)$$

or

$$w = A(s)^b$$

where A and B are constants and s is the space available per plant. On a yield per unit area basis, and including density rather than space, Warne's equation becomes

$$y = A(\rho)^{1-b}$$

Kira et al. (1953) obtained a linear relationship between the logarithm of total yield per plant and the logarithm of density in a soybean experiment. The form of equation they proposed was

$$\log w + a \log \rho = \log K \qquad (7)$$

or

$$w \rho^a = K \qquad \left(w = \frac{K}{\rho^a}\right)$$

where a and K are constants, a being termed the competition-density index. This equation is exactly analogous to that of Warne—the a and K of Kira et al. being comparable with Warne's b and A, respectively.

Strictly speaking, the only type of yield/density curve which this equation can describe is one where yield is still rising at the highest density. Such curves are illustrated in Fig. 6, where Kira et al.'s equation is fitted to some of Donald's data for different harvests of subterranean clover (Donald, 1951). It can be seen that as the yield/density curve approaches an asymptotic shape with the passage of time (Fig. 6B), the slope of the regression line becomes steeper and the value of a (the competition-density index) increases and approaches a value of 1 (Fig. 6A). However, if an asymptotic shape is reached, then, to describe constant yield at the high densities accurately, the competition-density index has to take the value of 1, and this then implies that yield is constant at all densities, i.e., the yield/density curve becomes a straight horizontal line (with value K). Or, from Eq. (7):

$$w \rho = K \text{ constant} = Y \qquad (8)$$

[The Japanese workers referred to Eq. (8) as the law of constant final yield (Hozumi et al., 1956)]. It is also of interest that a competition-density index greater than 1 implies that yield decreases with all in-

creases in density. Thus, on theoretical grounds neither the truly asymptotic nor the parabolic yield/density situation can be described. In some circumstances it may be possible to obtain a reasonably satisfactory practical fit to the former situation with a value of a fractionally less than 1, although this was not the case with Donald's data in Fig. 6.

Both Warne (1951) and Kira et al. (1953) emphasized the possible significance of their respective power constants b and a, in Eqs. (6) and (7). Warne said that the higher the value of the constant, the more the plant was dependent on the space available to it; whereas Kira et al. (1953) interpreted an increase in value of the constant as indicating a more thorough utilization of the space available to the plant. From the agronomist's viewpoint, the significance of these constants is most easily appreciated by considering the succession of yield/density curves already referred to in Fig. 6. It can be seen that the greater the value of a the further the yield/density curve has progressed from its initial competition-free situation. This progression is associated with a greater degree of competition, a greater degree of curvature in the relationship and, as Kira et al. said, a more efficient utilization of space. On this basis the
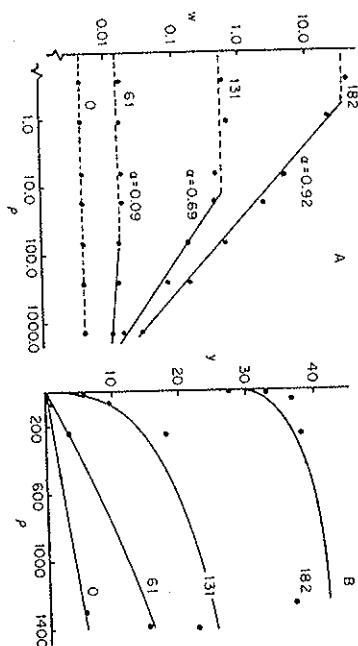

FIG. 6. The geometric ("power") equation (Eq. 7) of Kira et al. (1953) fitted to the total dry matter yield/density data of subterranean clover (Donald, 1951) at different numbers of days after sowing (0, 61, 131, 182): (A) The regression lines of w against ρ; dashed lines indicate densities at which there is no competition: w = g., ρ = plants/sq. lk. (B) The fitted yield per area/density curves: y = g./sq. lk.

agronomist can readily understand and compare relative differences in the values of these power constants that may have arisen due to differences in time, growing conditions, or plant species.

A further criticism of the geometric equation, first raised by the Japanese workers themselves (Shinozaki and Kira, 1956), is the failure of the equation to describe the leveling off in yield per plant at densities too low for competition to occur (indicated by the broken horizontal lines in Fig. 6A). This was a criticism of the exponential equations (Section II, B, 2), and it also applies to the reciprocal equations; its importance is discussed in Section II, B, 5, b.

5. Reciprocal Equations

The reciprocal equations are here regarded as those based on some mathematical relationship between the reciprocal of mean yield per plant and density. These represent a very important group of equations, which at present seems to offer the best possibilities of being able to describe yield/density relationships accurately and meaningfully. Since these equations are to be discussed more fully in Section II C, the present section serves only to describe their general characteristics.

a. Shinozaki and Kira. The first to propose a reciprocal equation were the Japanese workers Shinozaki and Kira (1956). This equation was derived from a simple logistic growth curve and the law of constant final yield (see Section II, C, 1, a). It was proposed by the Japanese workers because they had found that their geometric equation could not satisfactorily fit an asymptotic yield/density situation (Section II, B, 4). The form of equation derived was

$$\frac{1}{w} = a + b\rho \tag{9}$$

where a and b are constants. This relationship assumes a linear relationship between the reciprocal of yield per plant and density. Shinozaki and Kira (1956) tested this relationship in a number of asymptotic yield/density situations and found that it appeared to hold true in practice. However, this form of reciprocal equation cannot describe a parabolic yield/density situation.

b. Holliday. Holliday (1960b) was the first worker to propose that both an asymptotic and a parabolic form of yield/density relationship existed. Although it was pointed out earlier that his suggestion of the asymptotic form applying to total or vegetative yield and the parabolic form applying to reproductive yield may not be entirely valid, the two

equations which he proposed to describe the two forms of relationship are still of considerable interest.

Holliday (1960a) arrived at his asymptotic equation from yield/density studies on rape, kale, potatoes, and perennial ryegrass in which he observed that the reciprocal of yield per plant was linear with density:

$$\frac{1}{w} = a + b\rho \qquad (10)$$

where a and b are constants. Thus, this basic form of Holliday's asymptotic equation is identical to that of Shinozaki and Kira (1956), and it is of some interest that Holliday produced his largely from experimental observations whereas the Japanese workers derived theirs largely from mathematical considerations.

Like other workers, Holliday (1960a) pointed out that his equation could not allow for a constant yield per plant at those densities where there is no competition. He therefore termed the implied yield per plant at zero density the "apparent maximum" yield per plant and designated this A, which is equal to $1/a$ (see Fig. 7). He also suggested that a modified form of equation beginning at the density where competition first starts might be more accurate. Thus, if this density is n, and $\rho - n = m$ (see Fig. 7), Holliday's modification can in effect be written

$$\frac{1}{w} = a' + bm \qquad (11)$$

The reciprocal of a' would now equal the true maximum yield per plant (A'). However, Holliday admitted that, although more accurate biologically, this equation might be of limited use in practice because in any given situation A' would have to be determined experimentally.

Shinozaki and Kira (1956) suggested a rather different way of allowing for a constant yield per plant at densities free of competition. They proposed the inclusion of a factor δ in their basic relationship, so that

$$\frac{1}{w} = a + b(\rho + \delta)$$

They suggested that an appropriate value of δ should be chosen so that at high densities δ would be negligible compared with ρ and could therefore be disregarded, whereas at low densities δ would come into effect and

yield per plant would level off to a relatively constant and more realistic value. However, this factor δ seems to have no biological meaning and is included purely to try to improve the equation's goodness of fit at low densities. Moreover, since its value must depend on the maximum yield per plant without competition, then, like Holliday's A', it presumably could be satisfactorily determined only by experimental means in any given situation.
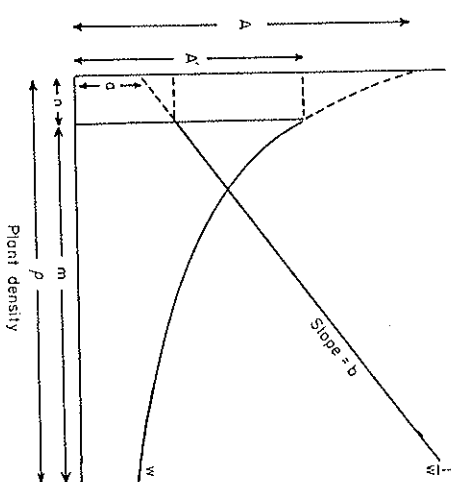

FIG. 7. Diagram of yield per plant (w) and reciprocal of yield per plant ($1/w$) plotted against density, illustrating the derivation of the asymptotic equation (Eq. 10) of Holliday (1960a) and its modification to allow for the absence of competition at low densities (Eq. 11); n is the density at which competition starts, A is the "apparent maximum" yield per plant, A' is the true maximum yield per plant.

Holliday (1960b) proposed that the parabolic yield/density situation, where the relationship between the reciprocal of yield per plant and density is no longer linear, could be described by the quadratic expression

$$\frac{1}{w} = a + b\rho + c\rho^2 \qquad (12)$$

where a, b, and c are constants. Holliday pointed out that the use of the quadratic was empirical, but this form of quadratic equation is a great improvement on the simple quadratic which Hudson (1941) applied directly to yield per area against density (Eq. 1). It produces a very flex-

ible parabolic yield/density curve which is not symmetrical about its point of maximum yield and which flattens off realistically at high densities. Some examples of this equation fitted to yield/density curves are given in Section II, C, 2.

c. *De Wit.* From studies of mixtures of barley and oats, de Wit and Ennik (1958) derived a single species yield/density equation based on a linear relationship between the reciprocal of yield per unit area and row width (where distance between plants in the row was constant). This took the form

$$\frac{1}{y} = a + bd_2 \qquad (13)$$

where a and b are constants, and d_2 is the row width. Expressed in terms of the reciprocal of yield per plant this equation becomes:

$$\frac{1}{w} = b + a\rho$$

which is exactly analogous to the reciprocal equation (Eq. 9) of Shinozaki and Kira (1956) and the asymptotic equation (Eq. 10) of Holliday (1960a).

Later, de Wit (1960) proposed a slightly different version of this equation based on a linear relationship between the reciprocal of yield per unit area and space available per plant. This is represented diagrammatically in Fig. 8, and the basic relationship is:

$$\frac{1}{y} = \frac{1}{P} + \frac{s}{PQ} \qquad (14)$$

or

$$y = \frac{PQ}{Q + s}$$

where s is the space available per plant and $1/P$ and Q are the points where the regression line cuts the $1/y$ and s axes, respectively. P is therefore equal to the asymptote of yield per area.

De Wit's later equation is again more readily compared with the other reciprocal equations if it is transformed to show the relationship between the reciprocal of yield per plant and density as follows:

$$\frac{1}{w} = \frac{1}{PQ} + \frac{1}{P}\rho \qquad (15)$$

It can be seen that this equation differs slightly from those of Shinozaki and Kira (1956) (Eq. 9) and Holliday (1960a) (Eq. 10), in that the value of $1/w$ at zero density $1/PQ$ is now defined by two constants instead of one, and one of these constants, P, is the asymptote of yield per area. The possible significance of this is discussed in Section II, C, 1, b.
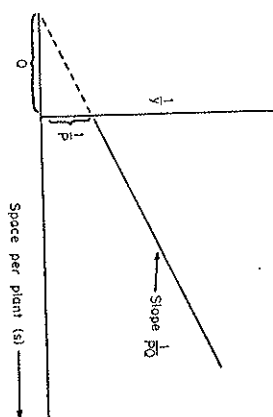

Fig. 8. Diagram of the reciprocal of yield per area ($1/y$) plotted against space available per plant (s) to illustrate the derivation of the reciprocal equation of de Wit (1960). $1/P$ and Q are the points where the regression line cuts the $1/y$ and s axes, respectively.

Like Shinozaki and Kira's equation, de Wit's can describe only an asymptotic yield/density situation; de Wit does not appear to have proposed any modification of his equation to describe a parabolic situation.

d. *Bleasdale and Nelder.* Bleasdale and Nelder (1960) proposed a reciprocal equation which they derived from a generalization of the logistic growth curve described by Richards (1959). This was originally proposed in the following form:

$$\frac{1}{w^\theta} = a + b\rho^\theta \qquad (16)$$

where a, b, and θ are constants.

This equation describes an asymptotic yield/density situation, but Bleasdale and Nelder pointed out that if the power on ρ exceeded the power on w the equation could also describe a parabolic situation. Equation 16 was therefore restated as

$$\frac{1}{w^\theta} = a + b\rho^\phi \qquad (17)$$

where ϕ is a constant.

This is the form of equation found in their subsequent references (Bleasdale, 1966b; Bleasdale and Thompson, 1966; Bleasdale, 1967); where yield is asymptotic, $\theta = \phi$; and where it is parabolic, $\theta < \phi$. In the last situation the yield curve flattens off along the density axis similarly to Holliday's parabolic equation (Eq. 12). The use of Eq. (17) was advocated by Bleasdale and Nelder (1960) because they disagreed with the division by Holliday (1960b) of yield/density relationships into vegetative and reproductive types. They preferred the use of a single generalized yield/density equation for all situations.

However Bleasdale (1966b) and Bleasdale and Thompson (1966) have stated that although there are theoretical reasons for allowing ϕ to have a value other than unity, it is the ratio of θ to ϕ which is important. Also, they considered that data are rarely accurate enough to enable specific values of both θ and ϕ to be determined. They therefore suggested that in practice it is sufficient to take the value of ϕ as unity. Thus Eq. (17) was restated as

$$\frac{1}{w^\theta} = a + bp \qquad (18)$$

Equation (18) is subsequently referred to as Bleasdale's simplified equation.

e. Farazdaghi and Harris. Farazdaghi and Harris (1968) have recently derived a yield/density equation from the same logistic growth curve used by Shinozaki and Kira (1956). However, these workers stressed that the law of constant final yield for total crop dry matter may not always hold true. [Farazdaghi (1968) has even shown that total dry matter in the sugar beet crop can be either asymptotic or parabolic depending on the environment.] Thus they modified the law of constant final yield to

$$w\rho^\gamma = K \qquad (19)$$

and derived an equation:

$$\frac{1}{w} = a + bp^\gamma \qquad (20)$$

This equation can describe either an asymptotic or a parabolic yield/density situation, depending on the value of γ; in the former case $\gamma = 1$, and in the latter case $\gamma > 1$.

C. A FURTHER EXAMINATION OF THE RECIPROCAL EQUATIONS

In Section II B the general characteristics of the different yield/density equations were discussed. The object of this section is to examine the reciprocal equations in more detail. These equations are singled out for this further examination for three main reasons: first, they are the only type of equation that can realistically describe both the asymptotic and the parabolic yield/density situations, either by means of different forms of equation (Holliday, 1960b) or by a single generalized equation (Bleasdale and Nelder, 1960); second, a good deal of biological meaningfulness has been claimed for them; and third, they have probably been used more than any other type of equation in recent years.

1. The Biological Basis of the Reciprocal Equations

a. Biological Derivation. (1) Shinozaki and Kira (1956), Bleasdale and Nelder (1960), and Farazdaghi and Harris (1968). Shinozaki and Kira derived their yield/density equations from the following assumptions on the growth of a plant:

(i) The growth of a plant can be described by a simple logistic growth curve.

$$\frac{1}{w} \times \frac{dw}{dt} = \lambda\left(1 - \frac{w}{W}\right) \qquad (21)$$

$$w = \frac{W}{1 + ke^{-\lambda t}}$$

where w is the weight of the plant at time t, λ is the coefficient of growth, and k is the integration constant. Both W and λ are assumed constant independently to time t.

(ii) λ in the above equation is independent of density.

(iii) Final yield per unit area is constant and independent of density.

On combining Eqs. (8) and (21) and determining the value of k when there is no competition at time zero, when the weight per plant is w_0, the reciprocal equation can be derived

$$\frac{1}{w} = a + bp \qquad (9)$$

where $a = e^{-\lambda t}/w_0$ and $b = (1 - e^{-\lambda t})/Y$.

Shinozaki and Kira (1956) go on to show that their reciprocal equation can be derived from more general growth curves, where λ and W are not independent of time, which would be an obvious objection. It was seen earlier that Farazdaghi and Harris (1968) used the same growth function as Shinozaki and Kira but did not assume the law of constant final yield (Section II, B, 5, e). On the other hand, Bleasdale and Nelder (1960) stated that they derived their equation from a generalization of the logistic growth curve given by Richards (1959) "with analogous arguments to those of Shinozaki and Kira."

The main interest in the biological derivation of these particular reciprocal equations lies in their application to the yield/density relationship of a plant part. Kira et al. (1956) had observed that the weight of a plant part could be related to the weight of the whole plant in the following way

$$w_p = k w^h \qquad (22)$$

or

$$\log w_p = \log k + h \log w$$

i.e., the logarithm of the weight of the plant part has a linear relationship with the logarithm of the total weight: log K is the intercept and h is the slope of the regression line. This is Huxley's law of relative growth, or law of allometry. Bleasdale (1967) pointed out that in its original context this law was applied to the relationship between plant part and total where plant size increased with age, whereas in the present context it is used to describe the relative changes brought about by density. From this allometric relationship, Shinozaki and Kira (1956) modified their original equation (Eq. 9) to describe the yield/density relationship of a plant part

$$\frac{1}{w_p^{\,h-1}} = a_1 + b_1 \rho \qquad (23)$$

This equation is very similar to Bleasdale's simplified equation (Eq. 18). It can describe a parabolic yield/density curve for a plant part, although, because of Shinozaki and Kira's initial assumptions of the law of constant final yield, this equation still assumes that the total yield/density curve is asymptotic. However, Shinozaki and Kira do not appear to have tested this equation in practice.

Bleasdale (1966a, 1967) also made use of the allometric relationship, which he stated in a slightly different form as

$$w = K w_p^l \qquad (24)$$

Combining Eq. (24) with his simplified equation (Eq. 18) he was able to derive a similar equation to apply to a plant part

$$\frac{1}{w_p^{\,\theta_p}} = a_1 + b_1 \rho \qquad (25)$$

where $\theta_p = \theta A$. Thus in the situation where $\theta = 1$, where the total yield/density curve is asymptotic, $\theta_p = A$. In this situation θ_p can therefore be estimated directly from the allometric relationship as the slope of the regression line. Bleasdale pointed out that this could allow the construction of the whole yield/density curve from only two densities: two estimates would enable θ_p to be estimated from the allometric relationship, and once this constant was determined Bleasdale's simplified equation for a plant part could also be fitted on two densities. (The dangers of fitting a yield/density curve on two densities were discussed earlier under Section II, B, 2.) The estimation of θ_p in this way also has another advantage, in practice perhaps a more useful one. As will be seen later, when fitting any reciprocal equation which contains a power it may be difficult to obtain an accurate estimate of this power. Thus, if in this instance θ_p can be estimated from the allometric relationship when total yield per area is asymptotic, Eq. (25) can then be fitted more accurately.

Although Farazdaghi and Harris (1968) suggested that their basic equation (Eq. 20) could be used directly for a plant part, they also derived a more meaningful equation using the allometric relationship (Eq. 24). This took the form

$$\frac{1}{w_p^{\,A}} = a_1 + b_1 \rho^\gamma \qquad (26)$$

They said that this described the way plant density affected the distribution of dry matter into plant parts. It is of interest that this equation is very similar to one of the original ones of Bleasdale and Nelder (1960) (Eq. 17), which had proved difficult to fit in practice. But Farazdaghi and Harris (1968) pointed out that if γ was estimated from their basic equation (Eq. 20) by fitting the total yield/density curve, this would then allow

the more complicated equation (Eq. 26) to be fitted, since only one power would have to be estimated from the regression analysis. However, it is noteworthy that A could also be determined from the allometric relationship (whether the total yield/density curve is asymptotic or not), although γ still has to be determined by fitting either Eq. (20) or Eq. (26). Also, it is of interest that the only situation in which the approach of Farazdaghi and Harris (1968) does not entail determining at least one power by directly fitting one of their yield/density equations is again when total yield is asymptotic, for in this case $\gamma = 1$ and A is obtainable from the allometric relationship.

It must be emphasized, however, that to make use of the allometric relationship, or to estimate γ in Eq. (20), it is necessary to have data for total plant weight as well as for plant part. In practice this may present difficulties. For example, in the cereal crop it may be difficult to obtain comparable estimates of grain yield and total dry matter since the latter may have declined from its maximum value before the maximum value of the former is achieved. A similar situation exists in the potato crop when total dry matter and final yield of tubers are considered. Also, where the plant part is not present throughout the whole life of the crop, the use of the allometric relationship may require further consideration. In view of these difficulties, the agronomist may frequently find that in practice he is not in a position to predetermine any power which he can substitute in the equations specially derived for fitting plant part data (Eqs. 25 and 26). He must then fall back on the use of either Bleasdale's simplified equation (Eq. 18) or Farazdaghi and Harris's basic equation (Eq. 20) and apply these directly to his plant part data. In this situation there seems little to choose between these two equations; they both involve fitting one power and they describe very similar yield/density curves.

(2) *De Wit (1960)*. De Wit's approach to the derivation of his yield/density equation is of interest because it differs markedly from the approaches seen in the previous section. De Wit termed his equation a "spacing formula," and he derived it from a consideration of the space available to a plant and the plant's ability to take up that space. He developed this formula from a consideration of two species grown on a homogeneous field of unit surface which he assumed to be divided into a number of squares of equal size.

In a first model he assumed that the growth of one plant was unaffected by the growth of another. Thus if a plant is grown in each square the yields of each species in different mixtures can be represented by Fig. 9A. However, de Wit pointed out that in practice this situation would occur only where the density was so low that there was no competition or where the competitive powers of the two species were equal.

De Wit developed his argument for the more practical situations where plants did compete. This situation is illustrated diagrammatically in Fig. 9B. It can be seen that the yields of species 2 are higher, and the yields of species 1 are smaller, than would be expected from the first model.
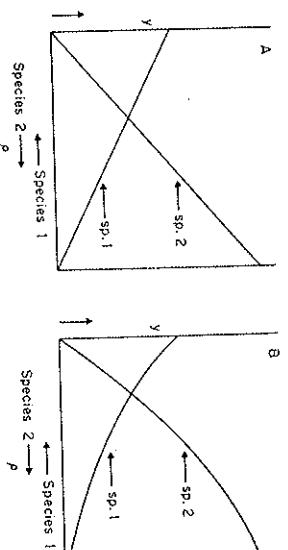

FIG. 9. Diagrammatic representation of the yields of each of two species (sp. 1, sp. 2) grown in different mixtures: (A) where there is no competition between the species; and (B) where competition exists between the species. At any point on the ρ axis, all the squares of the homogeneous field contain a seed either from species 1 or 2.

De Wit said this was because the plants of species 2 crowded the plants of species 1 out of some of the space alloted to them. He went on to consider the situation where only one species occupied some of the squares and the rest remained empty (i.e., the relationship between a single species and plant density). He suggested that this single species would now behave in a manner similar to the dominant species in a mixed situation in that it would occupy more space than was allocated to it. Thus the relationship between the number of plants and the yield of this species would be comparable with that observed for species 2 in the example above (Fig. 9B). De Wit assumed this relationship to be asymptotic and, using some oat data of Montgomery (1912), he derived the expression given earlier (Section II, B, 5, c). It might be questioned whether the now arbitrary choice of the size of the square might not affect the result of the spacing formula; however, de Wit showed that this was not the case.

It is of considerable interest that from this sort of approach de Wit developed an equation very similar to the other reciprocal equations. However, since de Wit has not suggested any modification of his equation to describe parabolic yield/density situations, the derivation outlined above is not examined in depth.

b. *Biological Validity of the Constants.* It has been shown previously that for the situation where the yield/density relationship is asymptotic the equations of Shinozaki and Kira (1956), Holliday (1960a), Bleasdale

and Nelder (1960), and Farazdaghi and Harris (1968) all become identical and can be written

$$\frac{1}{w} = a + b\rho$$

or, on a yield per area basis

$$y = \frac{\rho}{a + b\rho}$$ (27)

Thus as density increases, y approaches the value of $1/b$, i.e., the asymptote of yield per area $= 1/b$. If it can be argued that the asymptote of yield per area is a measure of the potential of a given environment, then b is a meaningful factor indicative of environmental potential. In the case of Bleasdale's simplified equation (Eq. 18), where θ does not equal unity, the interpretation of the value of b is less obvious, although perhaps it may still give some indication of environmental potential.

As the density tends to zero the value of yield per plant tends to $1/a$ in Eq. (27). It was seen earlier that this does not represent a very realistic situation for it ignores the fact that yield per plant levels off at densities too low for competition to occur (see Section II, B, 5, b). However, assuming that $1/a$ gives some indication of yield per plant in a competition-free situation then, by a similar argument to that employed for b, a can perhaps be regarded as a meaningful factor indicative of genetic potential. It is interesting to pursue this reasoning with de Wit's spacing formula

$$\frac{1}{w} = \frac{1}{QP} + \frac{1}{P}\rho$$ (15)

In this instance the asymptote of yield per area is P, and yield per plant appears to approach a value QP as density approaches unity. Thus in this equation maximum yield per plant, QP, is defined partly in terms of an environmental factor, P. This probably represents a more realistic situation.

Several workers have examined the time trend in these constants. Shinozaki and Kira (1956) found that the value of b in a soybean density experiment rapidly increased with time in the period just after germination, but thereafter it fell, rapidly at first and then more slowly, toward a constant value of b. Jones (1968) found a similar time trend in b for the dwarf bean crop. From a biological point of view it is hard to explain the

rapid rise in the value of b after germination. However, this may be an effect of the absence of competition affecting the fitting of the equation. Jones (1968) also found that the value of a fell throughout the season although there was a tendency to approach a constant value toward the end. Reestman and de Wit (1959) determined the course of P and Q in their equation (Eq. 14) throughout the latter part of the growing season in an experiment on sugar beet. Both P and Q increased with time and approached a constant value, Q doing so rather more quickly than P. With the exception of the changes in b at the early stages of growth, these time trends in the values of the constants are reasonably in accordance with what might be expected from their suggested biological significance.

Bleasdale and his co-workers have examined the effect of variety and environment on the values of a and b. Bleasdale (1966b) analyzed some yield/density data with Eq. (18) for three varieties of onions grown in the same environment. The values of a and b obtained are given in Table II, and these suggest that the value of a depends upon the variety. How-

TABLE II

THE VALUES OF THE CONSTANTS a AND b OBTAINED BY FITTING EQ. (18) TO THE YIELD/DENSITY DATA FOR THREE ONION VARIETIES[a,b]

Variety	a	b
Lancastrian	0.01117	
Runburger	0.01901	} 0.00263
Sutton A1	0.01706	

[a] After Bleasdale (1966b).
[b] The data were fitted taking a common value of $\theta = 0.8$.

ever, it must be emphasized that these differences in a were for a common fitted value of b, since Bleasdale did not find significant differences between the individual values of b. In the same paper Bleasdale stated that unpublished results with other crops suggested that the value of b varied according to the soil fertility, but the value of a did not; further that a appeared to be a constant from year to year for a given variety. This hypothesis was also borne out by work of Bleasdale and Thompson (1966) on parsnips. This idea was further investigated for some wheat data of Willey (1965) for which one variety was grown under a number of environmental treatments. The values of a and b obtained by fitting Eq. (18) are given in Table III. It can be seen that for all four treatments, fitted independently for a and b, a appears to be reasonably constant but b changes.

TABLE III

THE VALUES OF THE CONSTANTS a AND b OBTAINED BY FITTING EQ. (18) TO THE YIELD/DENSITY DATA FOR A WHEAT VARIETY[a,b]

	a	b
Control	0.109	0.0673
Treatment 1	0.105	0.0815
Treatment 2	0.097	0.1092
Treatment 3	0.108	0.0963

[a] After Willey (1965).
[b] The data were fitted taking a common value of $\theta = 0.5$. (Yield data are given in Table IV.)

Holliday (1960a) examined the meaningfulness of the constants in his equations in rather a different way. It was seen earlier (Section II, B, 5, b) that he appreciated the significance of the constant a and termed $1/a$ the "apparent maximum" yield per plant (A). Thus, substituting $1/A$ for a, the form of his basic asymptotic equation becomes

$$\frac{1}{w} = \frac{1}{A} + b\rho$$

which can be written

$$w = A \cdot \frac{1}{1+Ab\rho}$$

or, on an area basis

$$y = A \cdot \frac{1}{1+Ab\rho} \cdot \rho = \frac{A\rho}{1+Ab\rho}$$

He termed the expression $1/(1+Ab\rho)$ the "competition function," and it can be seen that the value of this decreases as density increases. Holliday considered that the definition of yield per plant as $A \cdot [1/(1+Ab\rho)]$ gave a realistic description of what actually happens in practice, for it indicates how the yield of a plant at any given density is a product of the potential of the plant (A) and the forces of competition that are acting upon it $[1/(1+Ab\rho)]$. Similarly, Holliday (1960b) expressed his parabolic equation as

$$y = A \cdot \left(\frac{1}{1+Ab\rho+Ac\rho^2}\right) \cdot \rho$$

In this case the competition function is $1/(1+Ab\rho+Ac\rho^2)$.

In conclusion, from the evidence presented it appears that it may be possible to ascribe some biological meaningfulness to the constants in the reciprocal equations. Thus, examination of these constants may help to pinpoint genetic or environmental components of yield/density relationships. However, it seems likely that the inevitable interaction of these two components is a far more complex situation than can be described by a few simple constants. It would therefore seem desirable that these constants should be examined in much more detail before any exact biological meaning is ascribed to them.

2. Statistical Regression Analysis and Goodness of Fit

In this section it is proposed first of all to consider some general points about the statistical fitting of yield/density equations. This is followed by a more detailed examination of the fitting of the reciprocal equations and the goodness of fit which they can give.

It should be emphasized that it is important to consider why the regression analysis is being carried out. Where the intention is merely to fit a smooth curve to some data points, the analysis can often be satisfactorily carried out on the yield per area/density data, as has been shown by Sharpe and Dent (1968). However, for reasons already given, for a more satisfactory description of the true yield/density relationship, it is usually more desirable to carry out the regression on the yield per plant/density data. An illustration of this is given in Fig. 10, in which two regressions have been carried out on the grain yield/density data of Pendleton and Dungan (1960). The simple quadratic equation (Eq. 1) is fitted directly to the yield per area data, and Holliday's parabolic equation (Eq. 12) is fitted to the yield/plant data. It can be seen that there is little difference between the regression lines as far as their ability to smooth the data is concerned but, at low densities particularly, the regression on yield per plant gives a much better description of the yield/density relationships.

The method which has usually been used to fit the yield/density equations has been a least squares regression. The reciprocal equations describing an asymptotic yield/density situation can be fitted by a simple linear regression, but with the introduction of powers or the use of the quadratic to describe a parabolic situation, the regression becomes more complicated. One of the assumptions on which the least squares regres-

sion rests is that the variation about any one point is the same as that about any other. This means that the variance of the yield values, whether it be yield per plant or yield per area, must be constant over all densities.
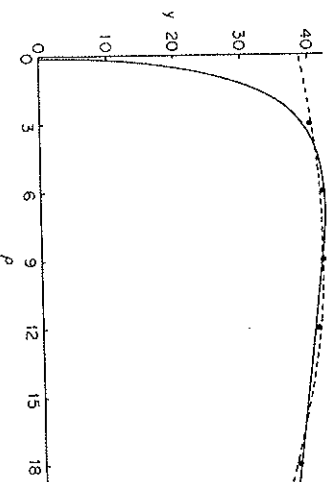
FIG. 10. The quadratic equation (Eq. 1) fitted directly to yield per unit area (——) and the parabolic equation (Eq. 12) of Holliday (1960b) (———) fitted via the reciprocal of yield per plant for the wheat data of Pendleton and Dungan (1960) meaned over four N levels and four varieties: y = bushels/acre, ρ = pecks/acre.

Keller and Li (1949) found this assumption to hold with their data for a density experiment with hops, but their range of densities was limited. Hozumi et al. (1956), when considering the individual yield of plants at three densities for leaf beet and turnips, found that the standard deviation of the points increased as plant size increased (with decrease in density), as shown in Fig. 11. Also, Nelder (1963) criticized the curve fitting of Jarvis (1962) for some lucerne density experiments and showed that it
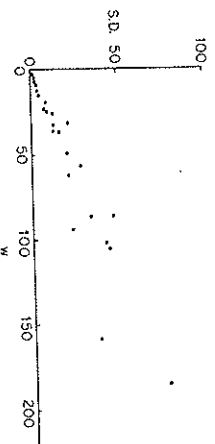
FIG. 11. A scatter diagram of the relationship between standard deviation (S.D.) and mean plant fresh weight of leaf beet, w (in grams), where changes in the latter were brought about by changes in plant density. (After Hozumi et al., 1956).

would be unlikely that the variation of yield per plant was uniform. He suggested that a more accurate assumption in yield/density experiments would be that the variance of the logarithm of yield per plant was constant. This assumption has been adopted by Bleasdale and his colleagues when fitting yield/density data to their equations. However, this assumption involves a more complicated treatment of the least squares regression than does the more usual assumption that the variance of w is constant.

The main interest in examining the goodness of fit of the reciprocal equations is in the parabolic yield/density situation since in the asymptotic situation they are identical. In this situation the most useful comparison would seem to be between one of the equations for which some biological validity has been claimed and Holliday's more empirical equation (Eq. 12). Since most workers are probably more familiar with the approach of Bleasdale and his co-workers than with the more recent one of Farazdaghi and Harris (1968), Bleadsale's simplified equation (Eq. 18) is compared with Holliday's.

When fitting Bleasdale's simplified equation, the assumption is made that the variance of log ($w^{-\theta}$) is constant; thus for a guessed value of θ, approximation to the true squares estimates of constants a and b can be obtained by a weighted regression of $w^{-\theta}$ with weights $\theta^2 w^{2\theta}$ (Nelder 1963; Mead, unpublished). The criterion of the goodness of fit is the residual sum squares divided by θ^2, and the best value of θ is that which reduces this to a minimum.

An example of some spring wheat data (Willey, 1965) (Table IV) fitted by the above method illustrates this in Fig. 12. For each of the four

TABLE IV

GRAIN YIELD DATA FOR A WHEAT VARIETY GROWN AT FOUR DENSITIES UNDER FOUR ENVIRONMENTAL TREATMENTS[a,b]

Density (10⁶ plants/acre)	Grain yield (cwt./acre)			
	Control	Treatment I	Treatment II	Treatment III
0.392	20.82	20.60	19.63	19.62
1.122	35.32	28.15	23.71	20.57
2.432	29.98	30.14	19.51	22.81
5.78	23.95	15.85	10.35	12.93

[a] After Willey (1965).
[b] Treatments: mean effect of reducing light intensity to 75 percent or 50 percent of full daylight during period of establishment—ear initiation (Treatment I), ear initiation—flowering (Treatment II), and flowering—harvest (Treatment III).

treatments fitted, a curve shows the goodness of fit (residual sum squares divided by θ^2) plotted against different θ values. From the graph it can be seen that there was quite a wide variation between the best-fitting values
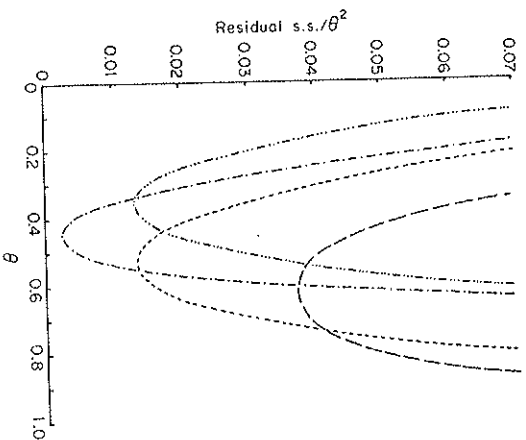

FIG. 12. An example of obtaining the best-fitting value of θ in Bleasdale's simplified equation (Eq. 18); the best fit is where the residual sum squares $(s.s.)/\theta^2$ is reduced to a minimum. Wheat grain yield data of Willey (1965): Control (—··—), Treatment I (———), Treatment II (———), Treatment III (———) (see Table IV).

of θ for each treatment. However, if a common value of θ of 0.5 was taken the individual θ's for the four treatments did not give a significantly better fit. The best values of θ were particularly well defined in these data, but this is not always the case. It may happen that the minimum is not so sharply defined, and in these circumstances it might be better to fit the correct but more complicated least squares regression of $\log (w^{-\theta})$ to avoid the approximation of the simpler weighted regression suggested by Nelder (1963); or this could be a situation in which Holliday's equation is of more practical use.

To make the comparison between Bleasdale's simplified equation (Eq. 18) and Holliday's parabolic equation (Eq. 12) valid, the latter is also fitted on the assumption that the variance of $\log (w)$ is constant. A comparison is made in Fig. 13 and Tables V and VI of the goodness of fit of

these equations to some selected data. The data are not meant to be comprehensive, but are chosen to illustrate the fit in two different parabolic situations, i.e., a definite parabolic situation (Table V and Fig. 13C and
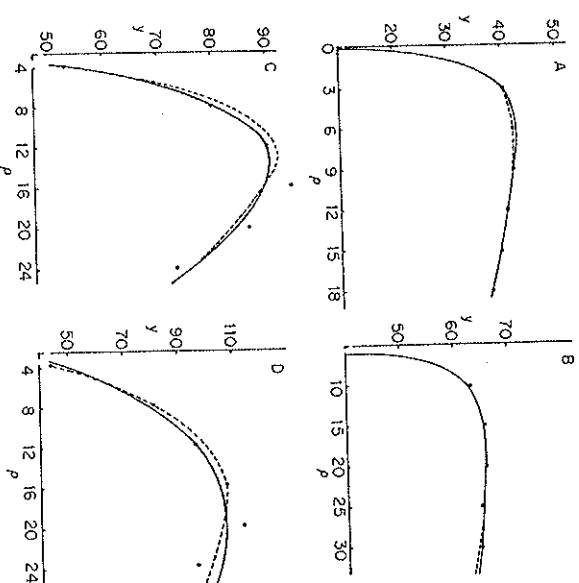

FIG. 13. Examples of Holliday's parabolic equation (Eq. 12) (———), and Bleasdale's simplified equation (Eq. 18) (———), fitted to some yield/density data where yield declines only gradually at high densities (A and B) and where yield declines quite sharply at high densities (C and D): (A) Grain yield of wheat (Pendleton and Dungan, 1960) meaned over four N levels and four varieties; y = bushels/acre, ρ = pecks/acre. (B) Grain yield of wheat, var. HILGENDORF meaned over four years (Crawford, 1964); y = bushels/acre, ρ = bushels/acre. (C and D) Grain yield of maize for hybrids WF9 × 38-11 and HY2 × OH7, respectively, at medium N level (Lang et al., 1956); y = bushels/acre, ρ = 10^3 plants/acre.

D) and a situation where there is only a slight decrease in yield at high densities (Table VI and Fig. 13A and B). The curves plotted in Fig. 13 are also represented in the respective tables. Although these data are very limited, it can be seen that there may be little difference on average between the two approaches, although one might be better than another for a particular set of data. It can also be seen that the ability of the equations to fit the data can vary considerably (compare Fig. 13A and B with Fig. 13C and D).

III. The Relationship between Plant Rectangularity and Crop Yield

It was emphasized in Section I that yield per unit area is dependent not only on the number of plants per unit area (plant density) but also on the spatial arrangement of those plants (plant rectangularity). Plant rectangu-

TABLE V

A COMPARISON OF THE VARIATION REMAINING AFTER FITTING EQS. (18) AND (20)[a]

A. Dumanovic and Penick (1962): Single-Cross Maize Hybrid Grown at 5 Densities and 4 Levels of Nitrogen

Nitrogen level (kg/ha.)	TSS	Equation (18): $\theta^b=0.45 \cdot RSS/\theta^2$	Equation (20) RSS
0	1.01	0.0154	0.0152
50	0.961	0.0231	0.0236
100	0.916	0.0275	0.0278
150	0.886	0.0272	0.0274

B. Lang et al. (1956): Three Maize Hybrids Grown at 6 Densities and 3 Levels of Nitrogen

Hybrid	Nitrogen level	TSS	Equation (18) $\theta^b=0.45 \cdot RSS/\theta^2$	Equation (20), RSS
HY2×OH7	Low	1.26	0.00809	0.00420
	Medium	0.721	0.0191	0.00847
	High	0.608	0.0128	0.0139
WF9×OH41	Low	2.30	0.0422	0.0341
	Medium	1.04	0.00878	0.00257
	High	0.218	0.00209	0.00173
WF9×38-11	Low	2.83	0.0236	0.0200
	Medium	1.48	0.00551	0.00770
	High	1.02	0.00767	0.00744

[a] RSS = Residual Sum Squares; TSS = Total Sum Squares. Both equations were fitted on the assumption the variance of log (w) is constant. The RSS/θ^2 obtained from fiting Eq. (18) are directly comparable with the RSS obtained from fitting Eq. (20).

[b] Value of θ which for the set of data as a whole reduced RSS/θ^2 to a minimum.

larity can be most easily visualized in a row crop where it can be defined as the ratio of the distance between plants within the row to the distance between the rows. In a broadcast crop it may be more generally defined as a measure of the unevenness of distribution. This rectangularity, or unevenness of distribution, is important because of the unevenness of competition which it produces; competition may be too intense between some plants and insufficiently intense between others.

TABLE VI

COMPARISON OF THE VARIATION REMAINING AFTER FITTING EQS. (18) AND (20)[a]

Study	TSS	θ^b	Equation (18) RSS/θ^2	Equation (20) RSS
Donald (1954)				
1. Winnera ryegrass grown at 5 densities for seed	30.2	0.90	0.0149	0.00292
2. Subterranean clover grown at 5 densities for seed	23.7	0.90	0.0394	0.0536
Crawford (1964)				
Wheat var. HILGENDORF grown at 5 densities for grain	0.72	0.85	0.0000806	0.0000947
Pendleton and Dungan (1960)				
Wheat grown at 6 densities for grain, average over 4 nitrogen levels and 4 varieties	2.33	0.75	0.000711	0.000234
Puckridge and Donald (1967)				
Wheat grown at 5 densities for grain	19.3	0.85	0.0171	0.0401

[a] RSS = Residual Sum Squares; TSS = Total Sum Squares about the mean.

[b] Value of θ which reduced RSS/θ^2 to a minimum for the particular set of data.

The extent to which rectangularity may effect the yield of a crop is clearly dependent on the plasticity of the individual plant, which in turn must be dependent on the plant species. However, the general pattern of effects is illustrated by some winter wheat data of Harvey et al. (1958) reported in Table VII. The treatments of Harvey et al. were not extreme, yet it can be seen that as rectangularity increases, either by increasing seed rate or increasing row width, yield per area gradually declines. Similar effects have been shown by Wiggans (1939) for soybeans, Reynolds (1950) for peas, Pendleton and Seif (1961) for maize, Bleasdale (1963) for peas, and Weber et al. (1966) for soybeans. Reynolds (1950) also showed that as rectangularity increases the optimum density may decrease (Fig. 14).

It would therefore seem desirable that equations describing the relationships between plant population and crop yield should be able to describe the effects of rectangularity as well as those of density. This can be particularly important because in the many population studies where different populations have been established on constant row width, rectangularity is not constant but increases with increase in density. Goodall (1960) attempted to fit the model

TABLE VII

THE EFFECT OF ROW WIDTH AND SEED RATE ON WINTER WHEAT GRAIN YIELDS (cwt./acre)[a]

Row width (inches)	Seed rate, stones/acre		
	5.5	11	17
4	43.9	43.9	43.6
8	43.0	42.5	41.4
12	41.6	41.4	38.0

[a] After Harvey et al. (1958).

$$w = ad_1^{b_1} d_2^{b_2} \quad (28)$$

or

$$\log w = \log a + b_1 \log d_1 + b_2 \log d_2$$

where d_1 is the intrarow spacing and d_2 is the interrow spacing. Thus $d_1 d_2$ is the space available per plant. Equation (28) is therefore an extension of Eq. (6).

Goodall fitted this model to some soybean data of Wiggans (1939) which covered a range of densities and row widths. He found a significant
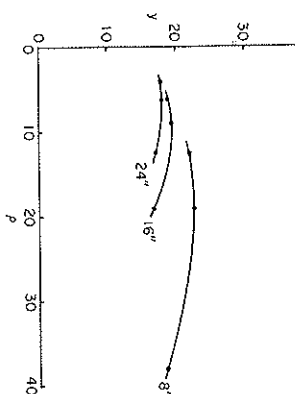

FIG. 14. The effects of rectangularity on the yield/density relationship in dried peas (Reynolds, 1950): the three curves represent different row widths, 8, 16, and 24 inches: y = cwt./acre, ρ = stones/acre.

difference between b_1 and b_2; he suggested that this was due to row orientation effects. Donald (1963) pointed out, however, that Eq. (28) has the undesirable characteristic that, if either of the power terms is greater than the other, then the optimum rectangularity at a given density would be obtained where the distance between plants was increased in one direction and decreased in the other. Berry (1967) criticized Goodall's fit to Wiggans' data, not only on account of the poor fit of log w against log d_1, but also because the values of d_1 and d_2 were not overlapping, and therefore different values of b_1 and b_2 could be expected.

Berry (1967) extended the simplified equation (Eq. 18) of Bleasdale and Nelder to take into account plant rectangularity

$$\frac{1}{w^{\theta}} = a + b\left(\frac{1}{d_1} + \frac{1}{d_2}\right) + \frac{c}{d_1 d_2} \quad (29)$$

Since $d_1 d_2 = s$, this model has included an extra term proportional to the square root of density. For a given density, w is greatest where $d_1 = d_2$, i.e., where rectangularity is 1:1, since $(1/d_1) + (1/d_2)$ is at a minimum value. This relationship gave a satisfactory fit to Wiggans' soybean data. Berry considered that for irregularly spaced crops, i.e., where the rectangularity is not constant, Eq. (29) might still be used as a first approximation from Bleasdale's simplified equation. For example, it could be used where plants are irregularly spaced within the row and rectangularity is defined by the mean intrarow distance and the interrow distance.

IV. The Variation in Yield of the Individual Plant

It was emphasized in the introduction that the variation in the yield of the individual plant has seldom been examined in yield/density studies. The analysis has been in terms of the mean yield per plant at a particular density with no consideration of the variation about this mean. Yet this variation can be of great importance wherever the size of the individual plant is an attribute of yield. For example, in Fig. 2D the effect of size grading on the marketable yield of parsnips can be seen at each plant density although the latter has little effect on total yield.

Kira et al. (1953), Hozumi et al. (1956), and Stern (1965) attempted to examine the effect of density and time on the variation in individual plant weights by calculating the coefficients of variation at each density. Kira et al. and Stern showed that the coefficients of variation increased with time, but the evidence was not consistent as to whether density affected the value of the coefficient of variation at any one time. However, Mead

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