

DETERMINATION OF CHARACTERS FOR YIELD SELECTION
IN SPRING WHEAT BREEDING PROGRAMS

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Peter B. E. McVetty

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ABSTRACT

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DETERMINATION OF CHARACTERS FOR YIELD SELECTION IN SPRING WHEAT
BREEDING PROGRAMS. Major Professor: L.E. Evans.

Three crosses of spring wheat (Triticum aestivum) currently included in the University of Manitoba wheat breeding program were used to evaluate the use of physiological and/or morphological parameters alone or in combination on F_2 plants or F_3 families as selection criteria to identify high yielding F_4 bulks.

The F_2 generation was handled as spaced plants grown in the field in two types of environments, (a) a stress-free environment and (b) a normal environment. Approximately 200 plants of each cross were measured for physiological, morphological, yield component and phenological traits as well as being visually rated for yield potential by 5 selectors. A random 50-seed sample from each of these plants was sent to Mexico in the winter of 1976-77 to generate F_4 bulks.

Groups of 49 for stress-free and 81 for normal environment grown F_2 's were returned from Mexico as F_4 bulks to be yield - tested in a six - replicate partially balanced lattice design.

The same 49 and 81 groups as tested in F_4 were grown simultaneously from F_3 remnant seed in the summer of 1977.

The results indicated that the most common single F_2 parameter which identified high yield potential in F_2 was visual yield selection, however the selection intensity had to be low in order to retain a majority of the high yielding lines.

A multiple regression analysis approach on a cross-specific basis was found to be better than a single F_2 parameter approach because a majority of the high yielding lines could be retained with a much higher selection intensity. The results were similar for the F_3 generation.

A combined cross analysis using multiple regression indicated that productivity and peduncle length in F_2 were the two most important common parameters. A prediction of high yielding lines based on these two parameters retained in excess of one - third of the high yielding lines with high selection intensity. However, no acceptable common parameters were found in F_3 and it was concluded that replicated F_3 yield tests would be more suitable in such cases.

Harvest index evaluation in a productivity and height framework retained a majority of the high yielding lines while allowing a selection intensity of approximately 15%. This technique involved the use of an optimum harvest index in productivity and height extremes of statistically characterized populations. It is concluded that the harvest index - productivity - height approach to selection will enhance the effectiveness of plant breeders in their search for high yield in spring wheat.

1. INTRODUCTION

"Cereal grains are the major food of mankind. In many of the less developed countries of the world, cereals provide two thirds or more of dietary calories. Rice in Asia, maize in South America, sorghum in Africa, and wheat in the Middle East are recognized as the staple foods on whose yields famine or feast depends. Among the developed countries there are many, such as Russia and Japan, in which cereals still provide more than half of the diet calories. Although cereals make a smaller direct contribution to the diet of developed countries such as the United States and Canada, total cereal use per person is extremely high. However, most of the grain is fed to livestock and becomes an indirect component of human diets.

World production of cereals over the last twenty years has increased more rapidly than has world population, but with more variation from year to year; for the world as a whole, increase in yield per unit area has contributed much more than increase in the area under cereal crops. This is particularly so in the developed countries, but in the less developed countries the rather smaller increases in grain production have been due about equally to increases in yield and in area.

The world average yield of cereal grains is 1.7 tonnes per hectare, more than twice as great as that of legume crops

and oilseeds. Partly because of their higher yielding ability, cereals are tending to displace the pulses in many less developed countries although they complement one another both agronomically and nutritionally. Also, the rate of increase in yield, on a world scale, is much greater in the major cereals than in the legumes, with the consequences that the cereals are becoming progressively more a predominant component of the world food supply.

Greater cereal yields are the key to increased food supplies given the restrictions on further increase in the area of land under crops. Improved agronomy, such as better weed control and more timely and effective fertilizer applications, has contributed greatly to the recent increases in cereal yields, as has better control of diseases and pests, whether by genetic or chemical means. Plant breeding has played a major role in three ways, 1) by the selection of disease and pest-resistant cultivars, 2) developing shorter-statured forms that do not lodge at high levels of fertilizer application, 3) and by selecting cultivars with greater yield potential which can respond to higher inputs. All three plant breeding approaches are essential and must be linked so it is difficult to partition progress among them. At low yield levels improved agronomy is most important. As fertilizer inputs increase, lodging resistance becomes more important, while in high input systems, increase in yield potential may be rate limiting.

There have been fashions in the emphasis given to

particular processes as the major limitation on cereal yields, and also to the stage of the crop life cycle regarded as most critical. Watson (1952) attached greatest importance to leaf growth, canopy development and leaf area index in the early stages of the crop. In subsequent years much more emphasis has been given to the final stages of the cereal life cycle since Archbold (1945) demonstrated that grain growth is largely based on current assimilation. As a consequence, particular attention has been given to crop photosynthesis through the grain-filling period as a major determinant of yield.

More recently, however, evidence has accumulated that the capacity to store assimilates in the grain may limit yields quite as much as the capacity of the crop to provide them during the grain filling period, Evans (1975).

The storage capacity of the crop is largely determined during the middle of its life cycle, in the period between inflorescence initiation and anthesis, partly by reproductive processes leading to the formation of the inflorescence and partly by the availability of photosynthate and nutrients at that time. In "source versus sink" arguments, it is important to remember that the potential size of the sink is largely determined by the photosynthetic assimilate supply at an earlier stage in the life cycle. Currently, therefore, more attention is being given to the middle "reproductive" stages of the cereal life cycle. But the plant breeder and the crop physiologist must consider all three stages - vegetative

reproductive and grain filling - because stable high yields will be obtained only when the yield - determining processes operating in all three are in balance with one another."¹

In this study parameters were measured relating to the three developmental stages of the spring wheat plant in F_2 and F_3 of three crosses and these have been related to F_4 bulk yield in simple and multiple correlation analyses and multiple regression analyses to attempt to determine if the efficiency of selection for yield in early generations of a plant breeding program can be increased by the use of applied crop physiology.

¹ Evans, L.T. and Wardlaw, I. F. 1976. Aspects of the comparative physiology of grain yield in cereals. Adv, in Agron. 28: 301-59.

2. LITERATURE REVIEW

2.1 Yield Components: The Early Approach to Scientific Plant Breeding

Although economic yield has been the main basis of selection in most crop breeding programs, there have been numerous attempts to find selection criteria based on the morphology, physiology and biochemistry of the development of crop yield.

In cereals, Engledow and Wadham (1923, 1924a and 1924b) were among the first to suggest a scientific approach to breeding for yield. They suggested the use of yield components, namely (i) average number of ear bearing tillers per plant, (ii) average number of grains per ear and (iii) average weight of a single grain in explaining yield differences in cereal varieties. They also investigated the usefulness of morphological and physiological parameters as indices of single plant yield. It was found that only "migration coefficient" (similar to today's harvest index only on a fresh weight basis) was of any real value.

The components of yield have continued to receive much attention from breeders.

Waldron (1929) reported a significant correlation between all the yield components and yield in common and durum wheats. He concluded that particular attention must be paid to keeping the number of kernels per head high to maximize yield.

Woodworth (1931) found that yield components in wheat were inherited independently and suggested that one could obtain good values of all the yield components in one genotype.

Bridgeford and Hayes (1931) concluded on the basis of a stepwise multiple regression analysis of yield components and agronomic characters in wheat that one should select for numerous big heads per row to increase yield.

Stephens (1942) in an attempt to overcome the yield plateau in oats in Great Britain by selecting for yield components concluded that component compensation largely ruled out yield improvement with this approach.

Frankel (1947) advocated the use of yield components to increase yield but only if this was done in replicated homozygous lines because the heritable variance of yield components relative to the environmental variance is too low to enable selection for yield components on a single plant basis.

Boyce, Copp and Frankel (1947) found that selection for yield via yield components in F_2 on a plotwise basis was successful in increasing F_3 family yield while selection for yield components on F_2 plants was unsuccessful.

Grafius (1956) introduced the concept of a geometric interpretation of the yield components and indicated that maximum yield is obtained at intermediate levels of the three yield components X, Y, and Z where X = number of panicles per unit land area, Y = average number of kernels per panicle and Z = average kernel weight. When $X + Y + Z = 3$, maximum yield

is obtained when $X = Y = Z = 1$. Since increases in the smallest component of yield will result in the largest yield gain, it seemed logical to take a good variety and attempt to improve its most limiting yield component.

Stoskopf and Reinbergs (1965) found that in oats and barley the number of grains per head was the most reliable yield component to use in estimating yield per plant. However, the authors go on to say that none of the three yield components can be used to predict yield on a plot basis and that although the three yield components effectively describe yield per plant they do not determine yield per unit area.

Quinlan and Sagar (1965) studied the effect of doubling seeding rate on the yield components of two varieties of wheat. In one variety tiller number was reduced by half while in the other both tiller number and grain number per spike were reduced; in both varieties seed weight remained constant.

Johnson et al. (1966) studied yield components in four winter wheats differing in height. It was found that yield components determined on a plot basis had no consistent relationship with yield per plot over the four varieties. They concluded that yield components are of little value to the plant breeder and that he should look at yield itself instead.

Adams (1967) dealt with a major pitfall of yield components - that of yield component compensation. He indicated that the negative correlations between yield components are due to strong interplant and intraplant competition. Correlations are low or near zero in plants under noncompetition

but are significant and negative for competitive plants. If these were true genetic correlations they would be much more constant. The author suggested that inputs of photosynthate to the sink are oscillatory and that yield component compensation results from the input level being high during some phases of sink development and low during others. Therefore the negative correlations of X, Y, and Z have little to do with establishment of actual yields. It is concluded that plant breeders should breed for an XYZ optimum.

Fonseca and Petterson (1968) arrived at conclusions completely contrary to those of Adams (1967) by studying yield components in winter wheat. These authors found that the majority of the variation in plot yield could be accounted for by its association with the three yield components. However they concluded that progress by selection for yield components per se may be limited by the strong negative correlations among the yield components.

Hsu and Walton (1970a, 1970b and 1971) studied yield components and agronomic characteristics in a 5 x 5 diallel of spring wheats and found that selection for agronomic traits associated with an increase in photosynthetic area above the flag leaf node would be more successful in increasing yield than selection for yield components.

Rasmusson and Cannell (1970) tested yield components as yield selection criteria in the early generations of barley crosses and found that supposed linkage between the yield components led to yield component compensation and made

selection for yield components unwise.

Adams and Grafius (1971) in commenting on Rasmusson's and Cannell's (1970) paper, disagreed with the idea of linkage in yield components and suggested that yield component compensation is due to the oscillatory response of sequential components to limited resources. Plant breeders were encouraged to select for yield advancement by selecting for optimal geometry of the yield components in their environment.

Knott and Talukdar (1971) studied the relationship between yield components on a plot basis and obtained a highly significant negative correlation between 1000 kernel weight and kernel number per plot. In spite of this negative correlation, they were able to increase yields by selecting for increased kernel weight.

Syme (1972a) conducted a study of greenhouse grown single plants of each of the forty-nine cultivars grown in the fifth ISWYN and found that 100 kernel weight was useful in yield performance prediction but not as good as harvest index or days from sowing to the emergence of the seventh leaf.

Walton (1972) found that yield components were useful in explaining yield differences in spring wheat varieties. The only trait which was better at explaining yield differences was leaf area duration.

Kaltsikes (1973) reported that in spring rye the yield components measured on a plot basis accounted for 97.3% of the variability observed in yield per plot in a stepwise multiple regression - and thus were good in explaining yield

variation.

Lee and Kaltsikes (1973) in a study of durum wheat, found that the yield components had high correlations with yield, and that the most important predictors of yield were number of kernels per plant, 1000 kernel weight and days to maturity. These parameters in a multiple regression equation accounted for 78% of the variation in yield.

The latest and most ambitious paper on yield components was by Grafius et al. (1976). They reported that in barley, selection of parents based on wide differences in yield components on a plot basis followed by one backcross to either parent resulted in advanced generations with yields which could be predicted quite accurately on the basis of parental yield component regressions. The authors attributed their success to the backcross which tended to preserve the integrity of an already proven system while adding factors from another system.

2.2 Growth Analysis

The second wave of scientific endeavor to simplify the search for yield was initiated by Watson in 1947. Growth analysis as used by Watson and others involved the use of sequential harvests of plant material throughout the growing season combined with an estimate of photosynthetic area or leaf area (LA) at each harvest. Parameters measured or derived from the analysis included leaf area index (LAI), leaf area duration (LAD), leaf area ratio (LAR), crop growth

rate (CGR), relative growth rate (RGR), net assimilation rate (NAR), and grain to leaf ratio (G).

Watson (1947) in a comprehensive comparative study of wheat, barley, potatoes, mangolds and sugar beets grown in one metre rows, investigated NAR and LA. He found a similar seasonal trend in NAR for all species but found significant differences in NAR between the species, with the rate increasing in the order wheat, barley, potatoes, mangolds and sugar beets. No significant varietal differences were observed in wheat. This was in contrast to LA, which varied significantly from variety to variety. Watson concluded that in general, variation in LA was the main factor determining differences in total dry matter (DM) production and yield, with variation in NAR being of minor importance.

Watson (1952) in a review paper of British results with growth analysis, covering NAR and LAI in wheat concluded that total DM production and yield were more dependent on LAI than on NAR. It was recommended that breeders attempt to increase yield by increasing LAI to a maximum or optimum while paying little attention to NAR.

Thorne and Watson (1955) reported that nitrogen application in any form at or near anthesis increased IAD and yield by 2% in Yeoman winter wheat. The G value remained nearly constant over all treatments and indicated that under British conditions yield is closely associated with IAD.

Lupton (1961) studying NAR in six wheat cultivars including tall and short varieties found significant differences

and suggested that these varietal differences should be of considerable interest to plant breeders.

Watson et al. (1963) carried out a complete growth analysis of new and old spring and winter wheats with the following results: (i) LAI of old winter wheats was higher than LAI of new ones, with this trend reversed for spring wheats, (ii) LAD of winter wheats was slightly greater than that for spring wheats but there were no significant differences in LAD between old and new wheats, (iii) NAR of spring wheats was greater than that of winter wheats, (iv) G values of new varieties were much higher than for old varieties and finally (v) yields of the two wheat types were equal.

Lupton et al. (1963) studied varietal differences in growth patterns of wheat and their importance in determining yield. Only shoot dry weight and LAD were significant in explaining yield variation in hybrid populations. When considering the prediction of yield from characters measured in a different season, the authors found the best correlation was that between the two estimates of yield itself.

Davidson (1965) controlled the LAI of Olympic wheat at 1 and 3, removed all leaves or half of all leaves at anthesis and compared these treatments with a control which had LAI 12. It was found that leaf removal at anthesis had no effect on yield while maintaining LAI at 1 and 3 reduced yield by 80% and 60% respectively. These treatments reduced yield by reducing both grain number per spike and mean grain weight by about 50%. The author recommended for Australian conditions

that IAD before ear emergence be given much greater attention than IAD after ear emergence. This is because Australian varieties senesce very rapidly in the increasing heat and drought before harvest.

Welbank et al. (1966) investigated the dependence of yield of wheat varieties on IAD in four British wheats. Grain yields were found to be nearly proportional to IAD of either the whole plant or just the flag leaf node and above after anthesis. The authors studied G values as well and found that they were nearly constant over all varieties and treatments and concluded that yield was more dependent on IAD than on NAR.

Fisher and Kohn (1966) looked at the relationship of grain yield to vegetative growth and post-flowering IA in the wheat crop (cv Heron) under conditions of limited soil moisture. Higher sowing rates, higher N applications or delayed sowing all decreased yield by increasing water stress in the plant before and after flowering and thus advancing maturity. Grain yield was found to be closely related to IAD after flowering ($.969^{***1}$). Grain yield was also correlated with total DM at flowering ($.875^{***}$). These results showed that IAD was important in determining yield and that there is an optimum level of vegetative growth for maximum yields in Australia.

Bingham (1967) experimented with three British wheats by artificially varying grain number per ear. The overall conclusion was that sink and source are equally important

¹*** = significant at .001