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PHYSIOLOGICAL BASIS OF ACHIEVING THE PRODUCTIVITY POTENTIAL OF WHEAT IN INDIA

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There has been considerable improvement in the yield of wheat during the past twelve years. This is reflected in the national averages of the various countries as well as the world average yield (FAO, 1972). In India, the national average yield of wheat was 640 kg ha^{-1} in 1950 but it reached 1400 kg ha^{-1} in 1978 (Fig. 1). In irrigated areas, such as Punjab, the average yield has increased from

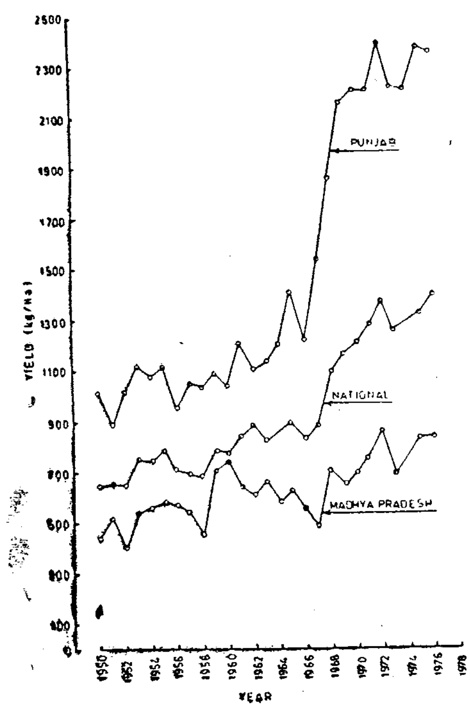

Fig. 1. Average yield of wheat in Punjab and Madhya Pradesh as compared to national average. (Source: Wheat Statistics Bulleltins, Govt. of India Publications)

1000 kg ha^{-1} in 1950 to 2400 kg ha^{-1} in 1978. As against this, in unirrigated regions such as Madhya Pradesh, the yield average has increased from 440 kg ha^{-1} to 840 kg ha^{-1}. It would be clear from figure 1 that possibly differenl factors have contributed at different times to raise yields to the present le ve.

Prior to 1966, the programmes of crop management played a significant role and thereafter the varietal improvement has been an important factor. It would be appreciated that whether the yield improvement occurred through management practices, varieties, particularly the plant architecture, or disease resistance, it had physiological basis. It could be that the present degree of improvement is the result of inadvertent selection for the desirable physiological and biochemical traits, because the seleccion for yield might have led to this. However, now the stage has reached when following questions are being asked:

1. What is the upper limit of productivity and what are the constraints in achieving this limit?
2. Have we reached plateau in the improvement of wheat and is no further improvement possible ?
3. Are the present day varieties most suitable for various inputs such as fertilizers and water, the factors limiting the yield?

We must confess that these questions are difficult to answer without some amount of theoretical analysis. Some very generalized estimates of maximum productivity have been made in the past considering insolation as the only factor under non-limiting conditions of other inputs (Loomis and Williams, 1963). It is here that theoretical estimates appear to give vast numbers as compared to the actual maximum harvests that have been obtained. In this review, we wish to consider the maximum production potential of wheat in relation to controllable and uncontrollable factors. The uncontrollable factors are the natural physical parameters such as insolation, day length and temperature. In addition, water and soil characteristics, though natural resources are only partly controllable. The choice of variety, fertilizers and other agronomic practices are manageable.

ESTIMATES OF MAXIMUM PRODUCTION POTENTIAL

Several attempts have been made to estimate the maximum production potential of various crop plants (Loomis and Williams, 1963, de Wit, 1967). According to Loomis and Williams (1963) a daily radiation of 500 cal cm^{-2} day^{-1} could produce a maximum of 71 g carbohydrate m^{-2} day^{-1} taking into account various radiation and metabolic losses. Penning de Vries (1974) estimated that a gram of carbohydrate produces 0·65 g of dry matter; therefore, the maximum dry matter production would be 46 gm^{-2} day^{-1}. Here, the main assumptions are that all light is being intercepted and there is no limitation of water or nutrients. However, the fact remains that during the growth period of about 150 days in wheat, from seedling stage to the final harvest, the total interception of light does not occur for more than 70 days; for 40 days it does not exceed 10%. For the remaining period the interception is about 50%. This works out to 4324 g dry matter m^2 (43·24 tons ha^{-1}) for the crop season of 150 days. Considering that 15% of the dry matter is in roots, the above ground production would be 37·76 tonnes ha^{-1}. If the harvest index is 45%, then a grain yield of 16·99 or 17 tonnes per hectare will be possibly the upper limit of wheat production. In some well planned and maintained experiments, yields upto 8 tonnes ha^{-1} have been obtained. Therefore, a maximum of 42·8% of the theoretical upper limit of yield has been obtained. If we take into account the yields obtained by Krishi Pandits, it would appear that more than 80% of the theoretical maximum has already been realised. In our own experiments we have obtained a maximum dry matter production of 19·0 tonnes per hectare of the above ground parts (Table 1). This is 50% of the upper theoretical limit. Let us now examine as to how so much dry matter is produced because this analysis may provide us the direction of research efforts to improve dry matter production

TABLE 1

Total biomass produced by some wheat cultivars

Cultivar	Biomass (tons ha^{-1})
NP 824	18.45
C 306	20.07
MG 197–8	20.25
MG 1–201	18.50
MG 191–24–1	19.10
MG 180–9	17.22
Average	18.93

DRY MATTER PRODUCTION

Dry matter production follows the usual sigmoid curve characterised by three distinct phases, namely, the lag phase, log phase and ripening or senescence phase. Indeed, most of the dry matter is accumulated during the log phase which overlaps partly vegetative and reproductive, particularly the post-anthesis, stages. Therefore, if we wish to increase dry matter production, one possibility is to reduce the duration of lag and/or ripening phases. These two phases are distinct in respect of physiological and biochemical status. In the lag phase, the problem is of quick development of leaf area whereas in the ripening phase (post-log phase) it is a question of slow or delayed senescence. In contrast to these phases, the log phase is characterised by development of full canopy and consequently of almost 100% interception of light. At this stage the leaf area index (LAI) is between 4 to 6. Any further increase in leaf area index does not necessarily result in increased dry matter production. Therefore, any increase in dry matter during this phase would have to be through increased net photosynthesis rate per unit area. In effect, the requirements of lag phase and log phase appear to be contradictory. But it is not so. The shortening of lag phase only means that the plants are able to develop a crop canopy capably of intercepting radiations completely as early as possible. This could be achieved through increased early tillering or faster expansion of leaf area. Since tillering and spike differentiation occur simultaneously, a time lag between these processes may be advantageous as will be mentioned in a later section.

PHOTOSYNTHETIC RATE

Where increase in drymatter production is required increase in the rate of photosynthesis would be a prerequisite. Photosynthesis studies on wheat species have indicated that the photosynthesis rate per unit area is higher in primitive wheats and is associated with smaller leaf size (Khan and Tsunoda, 1971). However, in case a genetical analysis of this character has to be made with a view to improve it, then it is necessary that the character is split into components and the genetics of various components studied Sinha and Khanna, (1975). In fact, variation among the hexaploid wheats has been observed which suggests that some old Indian wheat varieties have higher photosynthesis rate than the present day derivatives of 'Norin-10' dwarfs. However, it is essential that simple criteria using simple techniques are developed to screen a large number of genotyes under field conditions. Efforts are now in progress in this direction.

ACHIEVING HIGHER GRAIN YIELD

In the ultimate analysis, grain yield in wheat is the result of the number of ear bearing tillers (effective tillers), the number of grains per spike (ear) and the grain weight. If we wish to get a grain yield of 10 tonnes ha^{-1} we will have to work out options as follows:

Potential yield per ha^{-1} = Number of grains per ear × grain weight × Number of ears m^{-2} × 10,000.

If we fix 50 mg per grain weight as standard (50 g per 1000 grains weight), we need 20,000 grains m^{-2} to achieve the target of 10 tonnes ha^{-1}. For this there can be one of the following models:

10 tonnes ha^{-1} = 500 ears m^{-2} × 40 grain per ear × 50 mg $grain^{-1}$ × 10,000 *or* 400 ears m^{-2} × 50 grains per ear × 50 mg $grain^{-1}$ × 10,000 *or* 310 ears m^{-2} × 65 grains per ear × 50 mg $grain^{-1}$ × 10,000.

Now we could examine our existing varieties in relation to the above models. The characteristics of some varieties in this respect are given in Table 2. It would be seen from this data that some varieties do reach the desired level of ears/m^2 but fail to maintain either the seed weight or seed number. Alternatively, if some varieties maintain the characters of grain number and weight, they fail to maintain the desired number of ears/m^2. This, therefore, suggests the existence of competition among these components. Therefore, it is not surprising that in many instances negative correlations have been reported between these characters. If a simultaneous improvement in all the three components or even two of them has to be the objective, then we must clearly analyse the phenology of the plant and the importance of differentiation and development of these components. A detailed study of the development of yield components was

TABLE 2

Ear characters of some wheat cultivars

Cultivar	Ears m^{-2}	Grains/ear	Grain wt, mg
NP 824	447	55	44
Kalyansona	408	78	33
Moti	673	45	40

undertaken by us (Sinha *et al.*, unpublished). Some of the major findings based on 20 different genotypes belonging to *Triticum aestivum*, *T. durum*, triticale and barley are as follows:

1. At Delhi most genotypes have their mother shoot differentiated around 26 days from the date of sowing if the latter is between 2nd and 3rd week of November.
2. It takes about 15 to 20 days for the completion of the terminal spike formation and thus determining the number of spikelets.
3. It is around 26 days from sowing that the tiller development starts, although their initials may be laid earlier. Therefore, the period of tiller development and spike differentiation coincides.
4. The mother shoots bear a very small leaf area ranging from $18 \cdot 5$ cm^2 to $34 \cdot 0$ cm^2 at this stage. Therefore, there could be severe competition for photosynthetes between the growing spike and developing tillers.
5. It is in the period between completion of spike formation in the mother shoot and the emergence of the ear that the death of tillers occurs and the final number of tillers per m^2 gets determined.
6. The grain number and weight in the spike is determined after anthesis and is influenced strongly by water deficit, atmospheric drought and temperature during the post-anthesis period. At Delhi it takes about 35 days from anthesis to grain ripening.

Thus, it would be clear from the above that the development of spikelets and tillers overlaps, whereas the grain development phase is fairly independent. However, even in the latter case, increase in the number of grains per spike is associated with decreased grain weight. This again is suggestive of competition between these characters. According to some work in India, the early development of some particular grain in a ear could be responsible for slow development of others (Asana, 1975).

Let us consider that we have a genotype having potential of producing 100 grains per ear and also has the potential of achieving on an avereage 50 mg grain weight. This should result in the productivity of 5 g per shoot. However, what is required is 5 g dry matter consisting of carbohydrates, proteins etc. to realise the potential of 100 grains having an average grain weight of 50 mg.

In most studies it has been shown that photosynthesis rate of wheat leaves is about 30 mg CO_2 dm^{-2} hr^{-1} (Fischer, Wardlaw and Evans, 1975). In addition, it has also been shown that the flag leaf contributes most of the dry matter after anthesis towards grain development (Asana, 1975). The size of flag leaf in most instances varies between 14·0 to 35 cm^2. Assuming an average flag leaf size of 25 cm^2 and a photosynthesis rate of 30 mg dm^{-2} hr^{-1}, it should be possible to fix 82·5 mg CO_2 in a day of 11 hr effective light. This equals 56 mg carbohydrate or 36 mg dry matter per day. However, accepting that most of the accumulation in wheat is in the form of carbohydrates, we could possibly get 45 mg dry matter accumulation in grains every day. If the flag leaf remains functionally effective even for 30 days from the day of anthesis, the total accumulation would be only 1·35 g per ear. Therefore, decrease in the number of grains or the size of grains would be inevitable. In this calculation, we have made no provision for loss of dry matter through respiration. There are, however, some studies from control environment which have suggested that there is no limitation of photosynthesis (Evans, 1975). It could be that if one deals with genotypes having a potential of 40 or 50 grains per spike and 35 to 40 mg average grain weight it might appear that the photosynthate availability(source)is adeqeuate. However, many control environment studies have not been substantiated under field conditions (Begg and Turner, 1976) and it may not be surprising that this applies to the yield analysis of wheat also.

Nevertheless, if we fix a target 10 tonnes ha^{-1} of grain yield in wheat, with an assumption that there would be 400 or 500 ear bearing shoots per m^2 it becomes imperative that each ear has 2·5 or 2·0 g grain weight on an average. The present level of photosynthesis or the size of flag leaf do not seem to have this capacity. The following alternatives are possible:

1. Efforts could be made to increase the rate of photosynthesis and size of the flag leaf.
2. The contribution of the two leaves just below the flag leaf could be increased.
3. Photosynthesis of the ear could contribute to grain yield.
4. Greater mobilization of the reserves from the stem.

It is possible that in some cultivars one or more of these alternatives do operate. The important aspect at this stage, however, would be to establish this variability and its genetic control in wheat.

ROLE OF NUTRIENT AVAILABILITY

The assimilation of carbon is dependent upon the availability of nutrients in the plant. It has been observed that in several instances nitrogen is a limiting factor in obtaining higher dry matter production and yield. Other nutrients are equally important but several authors have considered NO_3 reduction as a rate limiting step (Hageman *et al.*, 1967). Several correlation studies have emphasized the importance of nitrate reductase as a selection criterion (Dalling and Loyn, 1977). There are several limitations in this respect which have been discussed elsewhere (Sinha, 1979). However, the main point remains as to what is the minimum intake and reduction of nitrate to obtain the maximum rate of photosynthesis or dry matter accumulation. Among the various types of wheat, the amount of nitrogen in different organs at the time of harvest is about 2%, 0·5% and 0·25% in grain, leaves and stem respectively. Therefore, it can be worked out as to what amount of nitrate is reduced during the life cycle of the plant. Most studies have shown that the amount of reduced nitrogen can be explained on the basis of NR activity. When we wish to increase dry matter production through increased rate of photosynthesis, it would be imperative that the uptake and reduction of nitrate is also enhanced. Alternatively, the assumption would have to be that the increase in photosynthesis rate would simultaneously lead to enhanced nitrate assimilation. Would it be due to some relationship between nitrate reductase and photosynthetic enzymes or due to the products of photosynthesis? An answer to this question is of vital importance.

UPPER LIMIT UNDER LIMITED WATER AVAILABILITY

The assimilation of carbon and accumulation of dry matter depend upon water availability. Studies in the past have shown that C_3 and C_4 plants utilise 600 and 300 g of water respectively for each gram of dry matter produced (Downes, 1969; Ludlow, 1976). Accordingly, if we wish to achieve the maximum limit of 42 tonnes ha^{-1} of dry matter production, it should require about 25,200 tonnes water ha^{-1}, equivalent to 2·52 tonnes m^{-2}. This equals 252 cm of water. This much amount of water neither would be available nor possible to apply. However, it is interesting that several agronomic studies have shown that a 50 q ha^{-1} grain yield or 12 tonnes ha^{-1} dry matter requires only 40 cm of water (Sinha and Singh, 1977). This means that water use efficiency of wheat under field conditions at Delhi is about 330 g water g^{-1} dry matter. Therefore, it is obvious that the results of water use efficiency are not necessarily applicable to field conditions. A still more important result was that varietal differences in dry matter accumulation, at equal level of water use, were observed. This, therefore, suggests the occurrence of variability for water use efficiency at the cultivar level. These observations have further been reinforced by studies on biomass production at different levels of water availability in *Triticum aestivum*, *T. durum*, triticale and barley. When water availability was reduced, the dry matter accumulation did not decrease in the same proportion. From the foregoing account it is clear that there is possibility of the existence of adaptive modification which could provide advantages under reduced water availability.

LIMITS OF WATER AVAILABILITY IN DRYLAND

From what has been stated about it is clear that if we knew the amount of available water, we can predict the upper limit of wheat production. In almost all parts of India, wheat is grown after rainy season on the moisture stored in the soil. Most soils have about 12 to 15% water holding capacity. Assuming that roots can tap upto 1·5 meter depth, it is possible to make use of

22·5 cm of water. In northern India we receive about 5 cm of rains during winter. Therefore, the total available water would be about 27·5 cm. However, all water from the soil profile is never utilized. In fact, it is rare that even 12 cm is utilized from 1·5 meter profile. Therefore, in all about 17 cm or 170 kg water is available per meter square in dry land. According to our estimates this should produce a maximum of 65 q ha^{-1} of dry matter or about 30 q ha^{-1} of yield. In fact such yields are commonly obtained in several experiments. However, the main question is whether a biomass greater than 65 q ha^{-1} can be obtained and secondly how best the grain yields can be improved.

In the first place, if water availability could be enhanced, there is a possibility of increasing dry matter production even without improving water use efficiency. Enhanced water availability is possible only when greater exploration of soil depth is achieved. This means that deeper root system could use more water and hence result in possibly greater dry matter production. Chaudhry (unpublished data) has in fact excavated living roots upto 220 cm soil depth. Therefore, it should be feasible to increase water availability through increased root growth. Selection for better root growth can be one of the major objectives while retaining other agronomically superior characters. In our studies on wheat, triticale and barley we have observed that the prostrate habit during seedling stage is advantageous under dryland conditions (Sinha *et al.*, unpublished). This could be due to better root characteristics of such types as suggested by Percival (1972). Another possibility is that we improve water use efficiency. This requires studies on the variability of this character in greater detail.

As regards better grain yield, it must be emphasized that 40 to 50% dry matter is produced after anthesis in wheat, and accounts for grain yield (Asana, 1975). In relatively controlled conditions Passioura (1976) has shown that the amount of available water at anthesis correlates strongly with grain yield. Therefore, we require a plant structure and crop canopy which should leave enough moisture at anthesis for grain development. Our experience now shows that there are some simple morphological adaptations which could satisfy the above requirements. However, we will have to prepare a good balance sheet of water availability to make use of such modifications. Thus, it should be possible to retain a reasonably high harvest index and hence grain yield under limited water availability.

CONCLUSIONS

In an effort to achieve the upper limit of wheat production, it is essential that the biological constraints in the functioning of the plant are eliminated. The elimination of constraints has to be in a manner that it eliminates competition between the number of tillers and the number of spikelets during early stages of growth. After ear emergence the competition between the number of grains per ear and grain weight is to be overcome. All this would require greater capacity to assimilate carbon and nitrogen. Therefore the following points can be made:

I. Increasing biomass production
- (a) Increase in photosynthesis rate
- (b) Selection for low respiration rate in relation to temperature.
- (c) High nitrate assimilation potential
- (d) Increased stomatal conductance.

II. Assuring better shoot number
- (a) Elimination of competition between spike development and tiller development.
- (b) Higher leaf area per shoot at spike differentiation.
- (c) Higher water potential at spike differentiation.

III. Assuring better grain yield/spike
- (a) High water potential of ear.
- (b) Higher photosynthetic contribution by ear.
- (c) Larger glume size.
- (d) More spikelets per ear.
- (e) Average grain weight about 45 mg.

Summary

An estimate of the upper limit of yield in wheat was made using radiation and light interception characteristics in a non-restrictive environment. It was estimated that a maximum yield of 17 tonnes per hectare could be the upper limit. It was concluded that today there is a limitation in achieving even the required dry matter and reduced nitrogen. In addition, the competition between the number of spikelets and the number of tillers before ear emergence and the number of grains per spike and the grain weight after ear emergence are major developmental constraints. Elimination of these constraints requires greater assimilation by shoots.

In conditions where water is a limiting factor, the yield potential should be assessed on the basis of available water. Since the grain development correlates strongly with the available water, the plant structure and population have to be adjusted in a manner as to leave sufficient moisture in the soil profile at anthesis. Here studies on the genetic variability in water use efficiency may be useful.

Various models for obtaining a 10 tonnes ha^{-1} yield have been suggested and several constraints have been identified which need attention.

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