# Effects of Past Breeding Efforts on Productivity Traits of Hard Red Spring Wheat

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Crop growth and productivity are the result of many complex physiological-biochemical processes. For this reason there are no 'yield' genes, since yield is dependent on the interaction of these processes, each controlled by genes, environment, and management practices. We have little control over the environment but can manipulate management practices and genes to improve the productivity of a particular crop. This article examines the role of plant breeding in altering the genes controlling the important physiological-biochemical processes that determine yield of hard red spring wheat.

## HISTORY OF NORTH DAKOTA HARD RED SPRING WHEAT YIELDS

Year-to-year variation in North Dakota wheat yields has been quite large due to many factors including rust epidemics, drought, and temperature. However, regression analysis of the state average wheat yields from 1900 to 1984 indicates that yields have increased at an increasing rate since 1930 (Fig. 1). At that time grain yields were about 11 bushels per acre and today's average yield is about 30 bushels per acre. Undoubtedly, changes in management practices have played a role in these increased yields. Examples include motorized equipment and later large equipment that allowed large areas to be seeded and harvested quickly, thus making better use of a relatively short growing season; herbicides (post-emergence and later preemergence) as an additional weed control method; and nitrogen fertilizer.

Improved varieties as a result of plant breeding also have played an important role in increasing North Dakota wheat yields. The wheat improvement program at North Dakota State University was initiated in 1911, which resulted in the first North Dakota released variety in 1926 and improved varieties at regular intervals thereafter. In addition, other wheat improvement programs in Canada and surrounding states have provided improved varieties that were used by North Dakota farmers. The utilization of winter nurseries, the semidwarf characteristic, modern plot equipment, and computers were important tools for the wheat improvement program, allowing for more rapid development of improved varieties.

The specific breeding objectives of wheat improvement programs during the past three-quarters of a century included improving or maintaining disease resistance, bread-making quality, and grain yield potential.

Crop disease can be an important determinant of yield and quantity. Stem and leaf rust have been two of the more important diseases in the spring wheat region, and efforts to maintain adequate resistance to prevalent rust races have consumed a large portion of the plant breeder's effort (3,4). Smith (3) concluded from an examination of leading hard red spring (HRS) wheat varieties in North Dakota from 1914 to 1976 that differential rust reaction was an important factor in nearly every major varietal change.

Most HRS wheat is utilized to make a form of bread. Although no single factor determines bread-making quality, the kernel proteins are especially important. Unfortunately, the relationship between grain yield and protein percentage among varieties generally is negative. Therefore, maintenance of adequate protein percentage and bread-making quality places a constraints on the improvement of yield potential.

A steady release of new disease resistant, high-quality varieties takes a great deal of the breeder's total effort. Nevertheless, raising the yield potential has been and remains an important objective.

The Fargo nursery or state average wheat yields compare varieties under management practices for which the cultivars were bred and grown, during high and low disease periods and under high and low environmental stress years. These comparisons show that HRS wheat yields have increased in North Dakota as a result of a combination of many genetic and management factors (Fig. 1). All of these factors have affected yields by altering physiological-biochemical characteristics of the varieties. However, the specific characteristics that limit yields are not well understood, and, therefore, have not been manipulated directly by wheat improvement efforts or changes in management practices. In addition, the reasons for yield improvements usually are not understood as the specific components involved generally have not been identified.

The next major factors allowing for future increases in wheat productivity are among the topics being researched today. Those that will be important contributors to yield improvement will probably include advances made through "genetic engineering" which would allow specific limiting processes to be improved through tissue culture and recombinant DNA methods. However, genetic engineering requires the identification of important physiological-biochemical processes limiting productivity. As part of our effort to identify the physiological-biochemical processes limiting efficient wheat production, we determined those processes altered by past breeding efforts to improve yield potential. To do this, we made direct comparisons among

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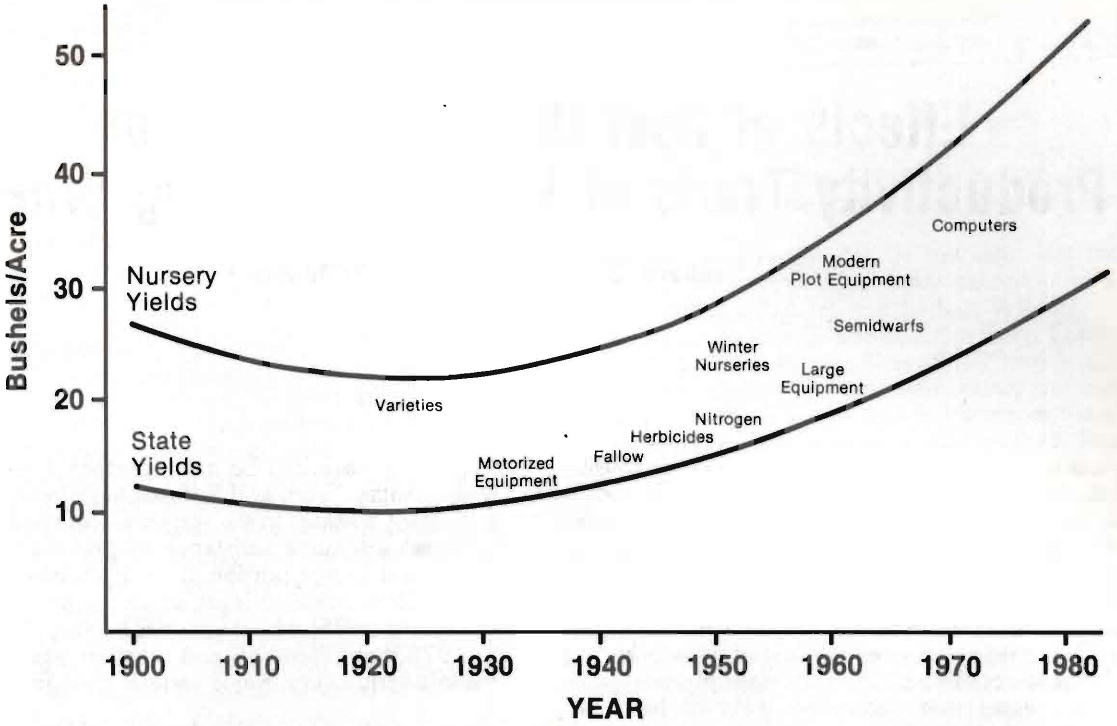

**Figure 1. Hard red spring wheat yields for the state of North Dakota and the Fargo experiment station nurseries as influenced by various management practices and varietal improvement factors.**

varieties representing genetic improvement efforts for the past three-quarters of a century.

## HISTORIC COMPARISON OF WHEAT VARIETIES

Twenty-one hard red spring wheat varieties were chosen to represent the past three-quarter century of wheat improvement in the Northern Great Plains (Table 1). These varieties were compared for one to three years in field experiments at Fargo to examine physiological-biochemical aspects associated with genetic yield improvements. Lodging was not a problem in these experiments and all varieties were protected by fungicide applications to minimize differential disease reaction as a factor.

Fifteen of the varieties were compared all three years. Regression analyses indicated a linear trend toward increasing grain yield but no change in total biological yield (Fig. 2). The 20 varieties tested the first two years indicated the same trends. Therefore, the increase in grain yield by genetic improvement efforts was a result of increased partitioning of dry matter to the grain (harvest index) rather than increased production of dry matter. These data suggest that the varieties developed in the 1950s, to obtain resistance to race 15B stem rust, exhibited lower grain yield potential. Apparently, this lower yield potential was due to a decreased production of dry matter rather than a decreased harvest index. Several years were required to compensate for the addition of these rust resistance genes and bring the production of dry matter back to the pre-1950s level. The grain yield data indicated that yield potential has increased an average of about 0.15 bushels per acre per year during the past three-quarters of a century.

Grain yield is dependent on 1) light interception, 2) utilization of intercepted light to produce dry matter, and 3) partitioning of that dry matter to the grain, whereas total yield is dependent only on the first two. The lack of a trend to increase total yield (Fig. 2) suggests that the first two traits have not been altered or have been altered in opposite directions. Wheat breeders have not selected directly for either light interception or utilizaiton, but selecting for traits

**Table 1. The leading hard red spring wheat varieties chosen to represent the past three-quarters century of wheat improvement.**

| Variety | Releasing agency | Year released for production | No. of years tested |
|---|---|---|---|
| Marquis | Canada | 1911 | 3 |
| Ceres | North Dakota | 1926 | 3 |
| Thatcher | Minnesota | 1934 | 3 |
| Rival | North Dakota | 1939 | 3 |
| Pilot | North Dakota | 1941 | 2 |
| Mida | North Dakota | 1944 | 3 |
| Lee | Minnesota | 1950 | 3 |
| Selkirk | Canada | 1953 | 3 |
| Conley | North Dakota | 1955 | 3 |
| Justin | North Dakota | 1962 | 3 |
| Chris | Minnesota | 1965 | 3 |
| Manitou | Canada | 1965 | 2 |
| Polk | Minnesota | 1968 | 2 |
| Glenlea | Canada | 1969 | 2 |
| Neepawa | Canada | 1969 | 2 |
| Waldron | North Dakota | 1969 | 3 |
| Era | Minnesota | 1970 | 3 |
| Olaf | North Dakota | 1973 | 3 |
| Kitt | Minnesota | 1975 | 3 |
| Butte | North Dakota | 1977 | 3 |
| Len | North Dakota | 1979 | 1 |

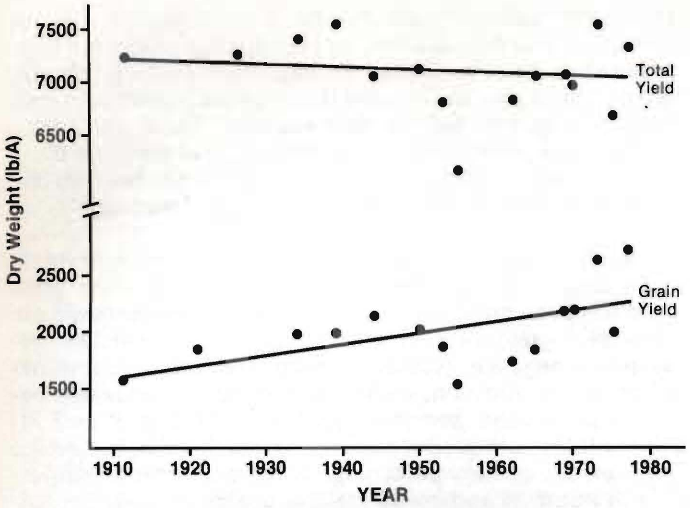

**Figure 2. Relationship between year released for production and grain yield or total yield of the 15 varieties tested for three years.**

such as "good leaves" could have altered either trait. Obviously, dry matter partitioning has played a role in grain yield improvement (Fig. 2), even though breeders have not selected directly for this trait. The more recent varieties partition about 40 percent of the total plant dry matter to the grain. Further grain yield improvement undoubtedly can be achieved by additional improvements in dry matter partitioning.

### Light Interception

Although the lack of an increase in total yield suggested that the end result of light interception and utilization have not been affected by breeding efforts, individual components of these two traits were evaluated to determine if specific changes have been made. Genetic differences were noted for each of the individual components, so improvement efforts potentially could have altered any of the components. The correlation coefficients in Table 2 measure the degree to which the plant characteristics vary with year of release. A significant (*) positive coefficient indicates that the plant characteristic increased as year of varietal release increased, and a significant negative coefficient indicates a decrease in the plant characteristic.

The correlation coefficient for heading date was not significant, indicating that there has not been a trend for past plant breeding efforts to result in earlier or later varieties (Table 2). Since differences in the length of the period between heading and physiological maturity were not observed, one could assume that breeding efforts have not altered the duration of light interception. However, the amount of light intercepted during the growing season is dependent not only on the duration but also on the amount of light intercepted per day, which relates to leaf development and size.

Wheat improvement did result in shorter and wider flag leaf blades. These effects on length and width altered the shape of the leaf blade but did not alter the flag leaf area (Table 2). In addition, the number of leaves per tiller and the number of tillers per foot of row were not altered by the wheat improvement efforts. Assuming the flag leaves are representative of the remaining leaves, breeding efforts have not changed the total leaf area. Since no trend to alter days to heading or total leaf area was observed, the pattern of leaf development was probably not altered. Therefore, as noted for the duration of light interception, past breeding efforts have not altered the amount of light intercepted per day.

**Table 2. Relationships between the light interception characteristics and year released of the 15 varieties tested for three years.**

| Characteristic | Correlation coefficient |
|---|---|
| Heading date | 0.178 |
| Flag leaf length | – 0.485* |
| Flag leaf width | 0.482* |
| Flag leaf area | 0.060 |
| Leaf number per tiller | 0.088 |
| Fertile tillers per foot of row | 0.126 |

*Ninety-five percent confident of a relationship between this characteristic and year released, indicating a trend to have altered this characteristic by past breeding efforts.

### Efficiency of Light Utilization

Several plant characteristics affect the efficiency with which the intercepted light is utilized. Plant height is one such characteristic, as a decreased height is frequently associated with less light distribution to the lower leaves. A trend to decrease plant height was observed (Table 3). This trend was linear for the past 75 years and not due only to the semidwarfs released since 1970.

**Table 3. Relationships between the light utilization characteristics and year released of the 15 varieties tested for three years.**

| Characteristic | Correlation coefficient |
|---|---|
| Plant height | – 0.680* |
| Nitrate reductase | – 0.605* |
| Glucose 6-P-dehydrogenase | – 0.090 |
| Glycolate oxidase | 0.130 |
| Malate dehydrogenase | – 0.020 |
| Phosphofructokinase | 0.175 |
| Ribulose bisphosphate carboxylase | 0.180 |

*Ninety-five percent confident of a relationship between this characteristic and year released.

A reduction in plant height would have both positive and negative effects on production efficiency. Negative effects include a reduced light distribution to the lower leaves. Positive effects include decreased lodging susceptibility and reduced plant inputs into stem material, a non-economic component. Therefore, the degree of height reduction probably shows a compromise between the negative and positive effects.

Biochemistry also is involved in determining the efficiency of light utilization. Plant growth is the net result of many interconnecting metabolic pathways, and enzymes regulate the flow of substances through these pathways. Enzymes are products of the genes, so breeding efforts could have unknowingly manipulated the action of these enzymes. To determine if breeding efforts altered enzyme activity, six enzymes that are thought to be important in regulating the growth of wheat were studied (2). Nitrate reductase estimates the biochemical potential to produce protein. Phosphofructokinase and malate dehydrogenase regulate dark respiration levels, and glycolate oxidase is important in photorespiration. Glucose 6-phosphate dehydrogenase regulates the flow through the oxidative pentose phosphate pathway toward nucleic acid synthesis, and ribulose bisphosphate carboxylase regulates the flow of carbon into photosynthesis.

Activities of the six enzymes were determined for the 20 varieties grown the first two years. The correlation coefficients for the relationship between enzyme activity and year of release indicated that a trend to alter enzyme action by breeding efforts occurred only for nitrate reductase (Table 3). Surprisingly, the trend was to decrease nitrate reductase activity, which would represent a decreased biochemical potential to produce protein. The practical reasons explaining why breeding efforts have tended to decrease the activity of this enzyme are not clear, but examination of the data does indicate that this apparent decrease in enzyme activity has greatly slowed or stopped in recent years (1). Nevertheless, the older varieties apparently were more capable of utilizing light energy for protein production than the more recent varieties.

### Partitioning of Plant Components to the Grain

As shown earlier, increased partitioning of dry matter to the grain has played a role in wheat improvement, even though wheat breeders have not selected directly for this trait (Fig. 2 and Table 4). Generally, an increased dry matter partitioning would be associated with an increased partitioning of protein although the amount of increase could differ, so an increased partitioning of protein to the grain by past breeding efforts would be expected. Protein is made up of many amino acids, and before protein can be translocated to the grain, it must be broken down into individual amino acids by the action of enzymes called proteases. The availability of amino acids for translocation as determined by protease action frequently limits protein partitioning. Therefore, it is reasonable to speculate that breeding efforts have altered the action of proteases.

Protease activities were determined at three-day intervals during grain filling for the 16 varieties grown in the third year (5). The pattern of activity started low at anthesis and increased about 400 percent during the grain filling period. The maximum protease activity or total activity during grain filling was not consistently altered by wheat improvement efforts (Table 4). That is, varietal differences were noted for both maximum and total protease activity, but there was no tendency for breeders to either increase or decrease the maximum or total activity by past breeding efforts. However, breeders did tend to increase the number of days required to reach maximum activity. The newer varieties required about four to six more days to reach maximum protease activity than did the older varieties. There was no apparent tendency to have altered the length of the grain filling period, so the tendency was toward a slower or delayed leaf senescence with no change in physiological maturity.

**Table 4. Relationships between the partitioning characteristics and year released of the 16 varieties tested the last year.**

| Characteristic | Correlation coefficient |
|---|---|
| Harvest index | 0.696* |
| Maximum protease activity | −0.216 |
| Total protease activity | 0.189 |
| Days to maximum activity | 0.565* |

*Ninety-five percent confident of a relationship between this characteristic and year released.

Past breeding efforts have tended to reduce kernel protein percentage (Fig. 3). This was not surprising, since grain yield has been improved, and the relationship between grain yield and grain protein percentage among varieties frequently is negative. However, breeding efforts have improved protein production, indicating a positive relationship between grain yield and grain protein yield (Fig. 2 and 3). Although protein production can be increased by increasing grain yields, protein percentage is the characteristic important in nutrition and bread-making quality. Protein percentage is dependent upon both the protein weight and the remaining kernel weight, so the decreased protein percentage indicates that improvements in protein partitioning to the grain has not kept up with improvements in dry matter partitioning. Perhaps the inadvertant decrease in nitrate reductase activity has played a role in the decreasing protein percentage.

Another possible explanation involves the improvement of harvest index without the improvement of biomass. About three-fourths of the grain protein but only one-half of the grain dry weight is in the vegetative plant parts at anthesis. High grain yield, then, depends on maintaining vegetative proteins involved in producing dry matter, and high grain protein percentage depends on degrading these same vegetative proteins. Therefore, improving both yield and protein percentage is difficult.

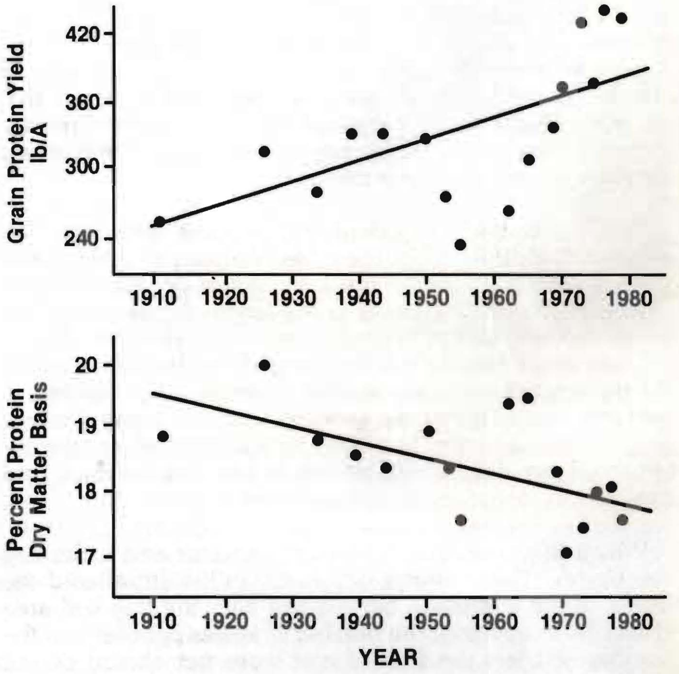

**Figure 3. Relationship between year released and grain protein percentage or yield of the 16 varieties tested during the third year.**

Two important factors affecting partitioning are the proper timing of the onset of senescence and the proper senescence rate. Apparently, breeders have inadvertantly altered these partitioning traits to improve productivity while causing only small reductions in protein percentage. Improving protein percentage without sacrificing grain yield potential probably will require an increase in nitrate reduction.

## SUMMARY

State average or nursery wheat yields have increased at an increasing rate since about 1930. Both improved varieties and management practices have played a role in bringing about the increased yields by altering certain physiological-biochemical characteristics of the crop. To determine those crop characteristics associated with increased yield potential, leading varieties for the past three-quarters of a century were compared in field experiments.

Grain yield is proportional to 1) light interception, 2) efficiency of light utilization, and 3) partitioning of dry matter to the grain. Apparently, the wheat breeders have increased genetic yield potential by improving the partitioning of dry matter, not by improving total dry matter production (light interception and utilization). The physiological-biochemical processes altered to achieve increases in dry matter partitioning included the protease enzymes associated with the timing and rate of senescence. This is a slow and difficult task since the partitioning characteristics desired for high grain protein percentage are not desirable for high grain yields.

The past improvements in genetic yield potential via increased dry matter partitioning have resulted in an improved plant efficiency. That is, the breeders have altered the plant to place more of the total plant dry weight and protein into the economic product (grain). Future improvements in yield potential also must provide further improvements in production efficiency. These future increases in yield potential will involve further increases in partitioning, but will increasingly depend on improved total dry matter production. Increasing total dry matter production by increasing only light interception could be counterproductive since most of the HRS wheat producing area is water limited. Increasing total dry matter by delaying leaf senescence will cause lower efficiencies and protein percentages because a greater proportion of the dry matter and protein will remain in the non-grain plant parts. Therefore, the challenge for future improvement in HRS wheat yield potential will be the identification and improvement of the plant characteristics limiting efficient utilization of the intercepted light.

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## REFERENCES

1. Deckard, E.L., R.H. Busch, and K.D. Kofoid. 1985. Physiological aspects of spring wheat improvement. In J.E. Harper, L.E. Schrader, and R.W. Howell (eds.) Exploitation of Physiological and Genetic Variability to Enhance Crop Productivity. Amer. Soc. Plant Physiol., Rockville, MD.
2. Henson, J.F. 1978. Enzymes and spring wheat improvement. PhD Thesis, North Dakota State University, Fargo.
3. Smith, G.S. 1978. Changes in North Dakota hard red spring wheat varieties, 1900-1977. North Dakota Farm Research 35:16-21.
4. Stoa, T.E. 1960. History of wheat variety changes on North Dakota farms for years 1945 to 1960. North Dakota Farm Research 21:17-21.
5. Stolz, B.J. 1980. Leaf protease activity in hard red spring wheat. MS Thesis, North Dakota State University, Fargo.