LONG-TERM GENETIC GAINS DERIVED FROM THE OKLAHOMA AGRICULTURAL EXPERIMENT STATION WHEAT BREEDING PROGRAM

By

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CHAPTER I

INTRODUCTION

Wheat (*Triticum aestivum* L.) ranks second to beef cattle as a source of income for Oklahoma agriculture. The state is second among the 42 wheat-producing states in winter wheat production and earned 300.5 million dollars from wheat export and products in 1992. Oklahoma wheat production increased from 101 million bushels (average yield, 26.0 bu/acre) in 1970 to 171 million bushels (29.0 bu/acre) in 1992, representing a 69.3% increase in total yield and a 11.5% increase in yield per acre (Oklahoma Dep. Agric., 1993). Much of this increase has resulted from the development of genetically improved cultivars in Oklahoma.

Since its beginning, the objective of the wheat breeding program of the Oklahoma Agricultural Experiment Station (OAES) has been to provide producers in the state with a continuous supply of wheat cultivars possessing high yield, acceptable test weight, earliness, bread-making quality, and resistance to prevalent diseases and insects. A major portion of the wheat acreage in Oklahoma is seeded to cultivars released by the OAES wheat breeding program.

Various government and private agencies provide funds in support of the program. A major portion of those funds is spent on testing experimental lines at several locations in the state over a period of years. Testing is necessary, but is expensive in terms of time and labor. We wanted to evaluate the testing and selection procedures used in this program, and to identify those which provide the greatest amount of genetic improvement or gain per unit of time for the least amount of resources.

Various approaches and procedures have been used to estimate genetic gains in wheat. Genetic gains have usually been measured by relative performance of cultivars in uniform regional nurseries (Schmidt, 1984; Schmidt and Worral, 1983), in intrastate performance tests (Feyerherm et al., 1984), or by growing cultivars from different eras in common environments (Cox et al., 1988). These approaches are quite informative for estimating genetic gains on a national or regional level, but of more immediate concern to the breeder is the long-term genetic gain realized in his/her program or specific stages thereof. The progress associated with each testing and selection stage of the OAES wheat breeding program has not been closely evaluated since the current system was initiated in 1969. This study was undertaken to estimate genetic gains in the OAES wheat breeding program over 24 years (1969 through 1993) of selection in two successive phases of multi-location testing trials. Grain yield, the primary selection criterion, was evaluated in both selection phases, while test weight and maturity (heading date) were considered as secondary traits in the second phase of selection.

CHAPTER II

LITERATURE REVIEW

Over the past 25 years, considerable increases have occurred in grain yield per hectare in almost all wheat-producing countries of the world. This change resulted from better management of inputs, such as fertilizers, irrigations, and pesticides, and from improved cultivars with higher yield potential. The largest increase in yields was noted in the mid 1950s to mid 1960s (Schmidt and Worral, 1983). It is still controversial whether that increase was mostly due to increased genetic potential of new cultivars or to reductions in yield constraints. Determining the "true" gain from breeding for yield based on evaluation of cultivars from previous breeding eras is often difficult under current production conditions (Dalrymple, 1980). Most researchers estimate (though not very precisely) that about one-half of the increase in yield can be attributed to improvement in cultivars and one-half to improved management practices.

Johnson (1986) reported that average world wheat yield from 1955 to 1979 increased by 680 kg ha^{-1}. Mexico, Romania, and Yugoslavia realized increases of more than 100% during that period while France, India, and the former USSR achieved greater than 90%. Yield advances in the four largest wheat-exporting countries (Argentina, Australia, Canada, and USA) ranged from 220 kg ha^{-1} in Australia to 630 kg ha^{-1} in the USA.

Waddington et al. (1986) conducted two trials at the Mexican Institute of Agricultural Research to determine the genetic yield potential of wheat cultivars released in northwest Mexico from 1950 to 1982. They reported that grain yield of those cultivars had risen by an estimated average of 59 kg ha^{-1} yr^{-1} or about 1.1% yr^{-1}.

Frey (1981) reported that during this century, the yield potential of wheat in the USA increased by approximately 50% as a result of genetic improvement. According to Salmon et al. (1953), improved cultivars accounted for 40% of the increased wheat production in the USA until 1950. Reitz and Salmon (1959) concluded that 10 to 30% of the increase in yield in hard red winter regions of the USA from 1931 to 1950 was due to genetic improvement. Auer and Heady (1968) estimated a total gain of 511 kg ha^{-1} in US wheat yields from 1939 to 1961; of this, 141 kg ha^{-1} was attributed to genetic improvement, 222 kg ha^{-1} to fertilizers, and 148 kg ha^{-1} to other sources. Jensen (1978) reported that the total gain in wheat productivity in New York could be divided nearly equally between improved technology and genetic improvement of cultivars. Hueg (1977) pointed out that not all the increase attributable to cultivars was due to genetic improvement for yield itself. He estimated that of the 51 to 56% increase in Minnesota wheat yields due to improved cultivars, 26 to 29% resulted directly from breeding for yield with the remainder due to incorporation of disease resistance. Silvey (1978) used annual records of the hectarage of cultivars and yields from national wheat trials, and reported an increase in yield of 84% in England from 1947 to 1975, 50% of which was attributed to improved cultivars.

Feyerherm et al. (1988) reported that wheat yields advanced 30 kg ha^{-1} yr^{-1} in the Great Plains of the US from 1954 through 1979. Of that increase, 43, 22, and 35% of the total was attributed to genetic improvement, applied N, and "other" sources, respectively. When the analysis was extended to 1984 for Nebraska, Kansas, and Oklahoma only, the average yearly increase was 32 kg ha^{-1} yr^{-1}. They also noted that the area planted to semi-dwarf cultivars in Oklahoma was only 38% by 1979 during a time when genetic improvement contributed 45% to yield gains. By 1984, the area of semi-dwarf cultivars increased to 76%; and the contribution of genetic improvement increased to 61%. According to Feyerherm et al. (1988), future genetic advances might result from increasing biomass in favorable environments and resistance to stress in unfavorable environments, rather than through major changes in stature.

Genetic gain in wheat yield has also been examined at the level of experimental strains submitted for testing by a regional cluster of breeding programs. Schmidt (1984) examined the data from nine Uniform Regional Wheat Nurseries in the USA from 1958 to 1980: 1) Southern Regional Performance Nursery (hard red winter wheat), 2) Northern Regional Performance Nursery (hard red winter wheat), 3) Western Uniform Regional Hard Red Wheat Nursery, 4) Uniform Regional White Winter Wheat Nursery, 5) Uniform Eastern Soft Wheat Nursery, 6) Uniform Southern Soft Wheat Nursery, 7) Uniform Regional Hard Red Spring Wheat Nursery, 8) Western Uniform Regional Spring Wheat Nursery, and 9) Uniform Regional Durum Wheat Nursery. Genetic improvement was lower for those nurseries grown in the harsher climatic regions of the Northern Great Plains and greater in the more productive regions of the Southern Great Plains. Combining all nurseries, yields increased consistently from 1958 to 1980 based on a 3-year average of 25% over the long-term check cultivars in 1959 to the same kind of average of 46% in 1979. That represented a total increase of 17% or an annual rate of gain of about 0.74%. In the Southern Regional Performance Nursery, the gain in yield was 30% relative to the check, 'Kharkof'. Schmidt and Worral (1983) also examined the data of the nine US Uniform Regional Wheat Nurseries from 1958 to 1982 to determine trends in yield improvement through genetic gains. They concluded that percentage increases in grain yield over the long-term check cultivar ranged from about 15 to 73% in these nurseries. In the Southern Regional Performance Nursery, performance of the highest yielding entry was considerably superior to that of the check, Kharkof, from 1960 to 1965, and then gradually plateaued at 45 to 50% gain with the advent of semi-dwarf cultivars in 1974.

Cox et al. (1988) evaluated 35 hard red winter wheat cultivars introduced or released between 1874 and 1987 in six Kansas environments to estimate genetic progress achieved by those wheat breeding programs. Linear regressions of cultivar means on year of release showed increases of 16.2 kg ha^{-1} yr^{-1} in grain yield, 0.4 kg m^{-3} yr^{-1} in volume weight, and 0.04 g yr^{-1} in thousand-kernel weight while days to heading (days after May 1) decreased at a rate of -0.1 d yr^{-1}. Rates of genetic gain varied significantly across environments. Since current hard red winter wheat cultivars are generally highly resistant to stem and leaf rust, the greatest gain in grain yield (1.4% of the experiment mean per year) was estimated during an epidemic of stem and leaf rust at two locations in 1986. A moderate gain per year (0.6%) was reported in most highly productive environments, and lower gain (0.4%) was estimated under drought stress. No gain was estimated when evaluations were conducted under an epidemic of tan spot disease, because current hard red winter wheat cultivars do not have resistance to that disease.

Feyerherm et al. (1984, 1989) used differential yielding ability (DYA), computed between cultivars and long-term checks in state performance trails, to measure the impact of genetic improvements from 1954 through 1979 and from 1979 through 1984. They reported increases of 368 kg ha^{-1} in Oklahoma during 1954 to 1979, and of 137 kg ha^{-1} during 1979 to 1984. They concluded that the impact of genetic improvement was inversely related to environmental constraints, that substantial yield improvement in unfavorable environments requires greater emphasis on stress resistance, and that no decline in the rate of yield improvement was evident.

Leslie (1991) and Clarke (1991) studied yield improvements in wheat due to the release of better adapted cultivars from 1975 to 1989 in Queensland using commercial and trial data, respectively. Leslie (1991) concluded that the most recent cultivars were 30% better than the oldest cultivars while Clarke (1991) estimated that improved cultivars had contributed a yield increase of 26%. Bull et al. (1993) examined productivity for wheat in Queensland from 1932 to 1987. They reported a gain of 1.76% yr^{-1} (20 kg ha^{-1} yr^{-1}) for 1932 to 1958 and a gain of 0.54% yr^{-1} (7 kg ha^{-1} yr^{-1}) for 1959 to 1987.

The above researchers have generally evaluated advances in genetic gain of wheat on a regional or intrastate basis. However, of more immediate concern to wheat breeders is the long-term genetic gain realized in their own breeding programs. Useful for this purpose, St. Martin and McBlain (1991) have developed a simple, but effective, statistical procedure for determining selection differential and genetic gain associated with each stage of a multistage testing program. While their application was to breeding lines submitted by several programs, the identical theory can be applied to a single breeding program as well. St. Martin and McBlain (1991) used the data from two testing stages, Uniform Preliminary Tests (UPT) and Uniform Tests (UT), of the cooperative regional soybean breeding program from 1960 through 1988 to determine genetic gain for yield, seed weight, and maturity. They found that selection differentials and genetic gains were small for all traits except grain yield. Selection differentials, genetic gains, and regression coefficients of genetic gain on selection differential for yield were 5.2%, 3.0%, and 0.59 in UPT and 2.8%, 1.7%, and 0.70 in UT, respectively. Selection differentials and genetic gains for yield were about twice as large in the UPT as in the UT. This is not surprising because many of the poorer yielders in the UPT would not be included in later UT. Similar statistics for maturity were -0.4%, -0.4%, and 0.84 in the UPT and 0.3%, 0.4%, and 0.84 in the UT. St. Martin and McBlain (1991) suggested that their procedure was applicable to multistage testing programs in any crop species, allowing breeders to examine their selection procedures by using existing data from their programs. Therefore, data collected from the Preliminary Yield Nursery (PYN), Intermediate Wheat Performance Nursery (IWPN), and Advanced Wheat Performance Nursery (AWPN) of the OAES wheat breeding program from 1969 to 1993 were analyzed to estimate genetic gain achieved in grain yield, test weight, and heading date.

CHAPTER III

MATERIALS AND METHODS

Data for this study were provided through the courtesy of Dr. Edward L. Smith, Wheat Breeder in the Agronomy Department of Oklahoma State University. The data were taken from three breeding nurseries constituting various stages of replicated, multi-location field testing prior to cultivar release. Each year, approximately 2000 $F_{3:4}$ and $F_{4:5}$ lines are evaluated in an observation nursery, usually grown in Stillwater and Lahoma, of the OAES wheat breeding program. Lines visually judged to be superior and high yielding are selected from the observation nursery for further sequential testing in the PYN, IWPN, and AWPN at several locations in Oklahoma. These nurseries constitute two consecutive phases of evaluation and selection followed by progeny testing: 1) Phase I, evaluation and selection in the PYN with progeny testing the following year in the IWPN, and 2) Phase II, evaluation and selection in the IWPN with progeny testing the following year in the AWPN. For Phase I, only grain yield (kg ha^{-1}) was recorded while for Phase II, grain yield, test weight (kg m^{-3}), and heading date (days after March 31) were recorded. At least two cultivars common to both years were evaluated with the experimental lines in a given phase. Selected progenies from the IWPN were often tested in more than 1 year of the AWPN to permit better decisions for cultivar release. For the purpose of this study, only the first year of the AWPN testing was used to determine selection response.

For determining selection differential for a trait in Phase I, three statistics were calculated from the PYN. They were: 1) $\bar{X}$ = the mean of all experimental lines, excluding check cultivars, tested in the PYN; 2) $\bar{X}_c$ = the mean of the check cultivars including only those also tested in the IWPN the following year; and 3) $\bar{X}_s$ = the mean of the lines selected from the PYN for further testing in the IWPN of the next year. The selection differential (I) was calculated as $I = \bar{X}_s - \bar{X}$. An estimate of genetic gain resulting from these selections was obtained by using two statistics from the IWPN the next year. They were: 1) $\bar{X}'_c$ = the mean of the check cultivars including only those common to the PYN the previous year; and 2) $\bar{X}'_s$ = the mean of the experimental lines selected from the PYN of the previous year and tested in the present IWPN. Genetic gain (G) for each pair of years in Phase I was then calculated as $G = (\bar{X}'_s - \bar{X}'_c) - (\bar{X} - \bar{X}_c)$.

In the same way, three statistics from the IWPN and two from the successor AWPN were used to estimate the selection differentials and genetic gains in Phase II. These were the mean of all lines, excluding check cultivars, tested in the IWPN ($\bar{X}$); the mean of the check cultivars, but only those common to the AWPN in the next year ($\bar{X}_c$); and the mean of the experimental lines selected from the IWPN for further testing in the AWPN of the next year ($\bar{X}_s$). The selection differential was calculated as $I = \bar{X}_s - \bar{X}$. Genetic gain associated with these selections was determined by using two statistics from the AWPN in the next year. These were the mean of the check cultivars in the AWPN, but only those common to the IWPN in the previous year ($\bar{X}'_c$); and the mean of the experimental lines selected from the IWPN of the previous year and tested in the present AWPN ($\bar{X}'_s$). Gain for each pair of years in Phase II was then determined by $G = (\bar{X}'_s - \bar{X}'_c) - (\bar{X} - \bar{X}_c)$.

It was not essential that the common check cultivars for a trait remain the same for both Phases I and II throughout the course of this study. Also, the common check cultivars could change across pairs of consecutive years in each stage. The only requirement was commonality of the check cultivars in two consecutive years of a selection stage. To allow comparison across pairs of consecutive years, selection differentials and genetic gains were expressed as a percentage of the mean of the corresponding checks as $I = [(\bar{X}_s - \bar{X})/\bar{X}_c]100$, and $G = [\{(\bar{X}'_s - \bar{X}'_c)/\bar{X}'_c\} - \{(\bar{X} - \bar{X}_c)/\bar{X}_c\}]100$. These percentages were averaged across

24 pairs of consecutive years.

The number of PYN, the number of lines tested per PYN, and the number of test locations varied from year to year. Generally, the number of PYN ranged from 3 to 12 per year, while the number of locations ranged from two to four. Altus, Goodwell, Lahoma, and Stillwater were the most common test locations for the PYN. Each PYN usually had 25 experimental lines and the same five check cultivars. The number of lines selected from the PYN for further testing in the IWPN ranged from 7 to 50 year (Table 1). The number of common checks for Phase I ranged from two to five. More than one common check cultivar were used in estimation of selection differentials and genetic gains to reduce bias caused by genotype-by-environment interaction.

Normally, a single IWPN consisted of 25 (in a few cases 30 to 35) lines selected from the PYN of the previous year and five to six checks. In some years, two IWPN nurseries were grown. The IWPN was grown at three to eight locations, with Altus, Goodwell (dryland), Goodwell (irrigated), Lahoma, Stillwater, and Woodward being the most common. The number of lines selected from the IWPN for further evaluation in the AWPN ranged from 2 to 20 year (Table 1). The number of common checks for Phase II ranged from 3 to 7 year. The AWPN consisted of 20 to 25 lines from the IWPN of the previous year(s) and 5 to 10 check cultivars, and was grown at 5 to 8 locations (usually at similar locations as of IWPN) of Oklahoma. Entries in all nurseries were arranged in a randomized complete block design, with usually four (but sometimes three) replicates per location.

The mean, variance, and standard error of I and G across years were calculated, giving equal weight to each year. Also, the regression coefficient (H) was determined by regressing G on I, using the no-intercept model, G = HI. The regression coefficient represents the proportion of phenotypic superiority realized as genetic gain and therefore is an estimate of realized heritability (St. Martin and McBlain, 1991).

The standard error of I was determined by

$$\left[\frac{\sum_{j=1}^{n} I_j^2 - n\bar{I}^2}{n(n-1)}\right]^{0.5} \qquad \textbf{(1)}$$

and the standard error of G by

$$\left[\frac{\sum_{j=1}^{n} G_j^2 - n\bar{G}^2}{n(n-1)}\right]^{0.5} \qquad \textbf{(2)}$$

where I_j and G_j are the selection differential and genetic gain for the jth year, j = 1, 2,....., n. The standard error of H was determined using the formula for the standard error of a regression coefficient associated with a no-intercept model:

$$\left[\frac{\sum_j G_j^2 - (\sum_j I_j G_j)^2 / \sum_j I_j^2}{(n-1)\sum_j I_j^2}\right]^{0.5} \tag{3}$$

A 3-year moving average for each nursery and for one long-term standard check cultivar was calculated from 1969 to 1993 to examine trends in nurseries with time relative to the current standard in commercial production. A 3-year moving average was employed to reduce potentially distorting individual year effects attributable to abnormal climatic factors. Two types of graphs were prepared to allow different comparisons over time. In one type, the 3-year moving averages for the nursery and standard check were graphed together to examine the performance of a specific nursery relative to the long-term standard check included in that nursery. Although the standard check for any particular year was the same across the three nurseries, slight differences among moving check cultivar averages in any 1 year reflected independent measurements of the same check cultivar in different nurseries. In the other type, the 3-year moving average of each nursery was expressed as a percentage of the corresponding moving check cultivar average, and the three nurseries were graphed together. This presentation allowed direct comparison of different nurseries for the same trait. Tabular data for these graphs (Fig. 1-10) appear in the Appendix. Because a single long-term standard check cultivar was not used in all years (1969-1993) for any nursery, one of the four checks ('Chisholm', 'TAM W-101', 'Payne', and 'Scout 66') tested in different periods were used for estimating the 3-year moving check averages. Scout 66 was used as a check from 1969 to 1972, TAM W-101 from 1972 to 1981, Payne from 1979 to 1987, and Chisholm from 1983 to 1993. In all three nurseries, the 3-year moving check average for 1971 is the mean of Scout 66 in 1970 and 1971 and of TAM W-101 in 1972. The 3-year average for 1972 was obtained from the mean of Scout 66 in 1971 and of TAM W-101 in 1972 and 1973. Similarly, the 3-year average for 1982 was calculated from the mean of TAM W-101 in 1981, Payne in 1982, and Chisholm in 1983. The 3-year average in 1983 was the average of Payne in 1982 and Chisholm in 1983 and 1984.

CHAPTER IV

RESULTS AND DISCUSSION

Calculations are illustrated for estimating selection differential and genetic gain (actual and percentage of common checks) for grain yield in Phase I and II (Table 2) reported in the annual reports of the OAES wheat breeding program (unpublished data). There were eight PYNs in 1991, each grown at three locations in Oklahoma: Goodwell (dryland), Lahoma, and Stillwater. Each PYN was comprised of 25 lines and five check cultivars. Of the total 200 experimental lines, seven were selected and were advanced to the successor test, IWPN, in 1992 for further testing. There were five common check cultivars (Agripro Mesa, Chisholm, Karl, TAM 200, and 2180) in the 1991 PYN and 1992 IWPN. The 1992 IWPN was grown at 4 locations in Oklahoma, Altus, Goodwell (Irrigated), Lahoma, and Stillwater. Of 33 lines tested in the 1992 IWPN, 20 were selected and advanced to the AWPN in 1993 for further testing. The AWPN in 1993 was grown at Cordell, Goodwell (dry), Goodwell (irrigated), Lahoma, Stillwater, and Tonkawa. There were seven common check cultivars (Chisholm, Cimarron, Karl, Mesa, TAM 200, 2163, and 2180) in the 1992 IWPN and 1993 AWPN.

For Phase I, the selection differential on a percentage basis (9.4%) was determined as the difference between the mean of seven selected experimental lines from the 1991 PYN (102.5%) and the overall 1991 PYN mean (93.1%). The genetic gain (12.0%) was determined as the difference in mean of seven lines tested in the 1992 IWPN (105.1%) (selected in the 1991 PYN) and the mean of the entire 1991 PYN population (93.1%), after adjusting for the mean of the respective common checks in each year. The importance of repeating this calculation across several pairs of years is underscored by the unexpected higher value for genetic gain than for selection differential. In Phase II, the selection differential and genetic gain obtained were 6.0% and -3.5%, respectively. The negative sign of genetic gain in Phase II indicates that the selections tested in the 1993 AWPN did not perform well relative to the 1992 IWPN population from which they were selected.

Selection differentials and genetic gains for grain yield in Phase I (PYN to IWPN) were estimated in consecutive years from 1969 to 1993 (Table 3). As expected, since selection was primarily for grain yield, selection differentials were consistently positive throughout the period examined, while genetic gains were more variable. Negative gains were observed in six years, but the absence of genetic gain was not the result of unusually small selection differential. For example, the selection differential was largest in 1992 (22.1% of the check mean), but the subsequent gain in 1993 was negative. No apparent decline in gain for grain yield has occurred in recent years of the breeding program indicating a yield plateau has not been reached. The highest gain of 12.9% was recorded in 1987-1988, and similar gains (12.4 and 12.0%) were found in 1974-1975 and 1991-1992, respectively. Years of high genetic gain were usually preceded by and/or followed by a year of much lower (if not negative) genetic gain.

Genetic gains for yield realized in the AWPN as a result of selection in the IWPN were also quite variable across the 24-year period, but were generally positive (Table 4). As expected for the primary trait of selection, selection differentials were positive in all years, ranging from 3.9 to 13.2% of the check mean. Negative genetic gains were found throughout the 24-year period and not concentrated in recent years of the breeding program. It is interesting to note that negative genetic gain for yield in Phase II occurred in those years preceded by either negative or extremely high positive gain in Phase I, while the highest positive genetic gains observed in Phase II were preceded by negative gain in Phase I. The highest gain (21.0%) was observed as late as 1992. Gains were more sporadic in this stage than in Phase I as positive gains never occurred in more than three consecutive years. In

Phase I, genetic gain was positive for as long as nine consecutive years (Table 3).

In addition to quantitative estimates, genetic gains were visually evaluated based on the mean performance of all lines tested in each nursery relative to a common long-term standard cultivar. The 3-year moving average for gain yield of each PYN was consistently lower than that of the common check prior to 1985 (Fig. 1). This was expected since the PYN represents the initial stage of replicated and multi-location field testing in the breeding program. Selection is based only on visual characteristics prior to the PYN. Long-term selection in the breeding program has resulted in yield means for the PYN which currently exceed the yield of a widely grown cultivar, Chisholm. Since 1991, the PYN mean has exceeded the standard cultivar by > 5.1%, although the mean yields of both have sharply declined since 1989.

Likewise, the moving-average grain yield of the IWPN remained consistently lower than that of the standard cultivar prior to 1985 (Fig. 2). Since that time, however, the mean of the IWPN has exceeded the standard cultivar. Despite the relative gain in nursery mean, the absolute yields of both IWPN and standard cultivar have declined since 1980 to levels recorded at the inception of organized yield trials in the OAES wheat breeding program in 1969. Marked shifts in disease pressure could explain the yield decline, and might serve as a focal point in determining its cause. Average yield performance of advanced lines in the AWPN surpassed the standard cultivar at an earlier stage in the breeding program than either the PYN or IWPN (Fig. 3). AWPN performance was lower than the standard cultivar from 1970 to 1981 except in 1975. Since 1982, the AWPN has generally exceeded the standard cultivar in grain yield, but the yield level has gradually declined since 1980 as found for the PYN and IWPN.

Three-year moving average yields of the PYN, IWPN, and AWPN were also expressed as a percentage of the same standard cultivar independently measured in each nursery (Fig. 4). Their relative performance should reflect the different stages of selection in the breeding program, with the PYN in the least advanced stage and the AWPN representing the most advanced. The AWPN had higher yields than the PYN or IWPN, and the AWPN exceeded the standard cultivar for a greater number of years (10 vs. 8 and 4 years for the IWPN and PYN, respectively). The most interesting feature conveyed by Fig. 4 is the change in disparity among nurseries over time. Following an initial short period of low disparity in grain yield among nurseries (1969 to 1972) and a long period of wide disparity (1972 to 1988), the relative grain yields of all nurseries have recently converged in the 1990s to similar levels (105-111% of the standard cultivar, Chisholm). This does not imply, however, that future gains are unlikely, because the yield of each nursery continues to increase.

Historically, a high priority of the OAES wheat breeding program has been to develop high yielding wheat cultivars with increased test weight and appropriate maturity (as measured by heading date). A test weight of 60 lbs bu^{-1} is considered the standard for market grain quality of wheat. The market grading, nutritive value, and milling quality of wheat grain depend on test weight, and a discount is usually applied if the test weight is below 60 lbs bu^{-1} (Krenzer and Doye, 1988). Test weight usually decreases with kernel deformation, especially by shriveling, due to genetic factors and/or environmental stresses during grain filling. Even though test weight was a secondary trait for selection in Phase II of the breeding program, selection differentials were positive in all years except for slightly negative selection differentials in three years (Table 5). These negative selection differentials also resulted in negative genetic gains for test weight. The largest selection differential (2.8% of the check mean) was early in the testing program (1970) and has since not exceeded 2.0%.

Genetic gains for test weight in Phase II were negative or zero for 11 years. Negative gains for test weight were observed in the same four years in which gains for yield were also negative in Phase II of the breeding program. As reported by Pixley and Frey (1991) in oat populations, this is consistent with the positive correlation of test weight with grain yield, though a number of other researchers like Souza and Sorrells (1988) have reported negative correlations between test weight and grain yield. Usually negative genetic gains were observed in two or more successive years, but were followed or preceded by high positive gain. Genetic improvement has not been made for test weight in three of the last four years of selection.

The 3-year moving average of each IWPN was compared with that of the standard cultivar to evaluate long-term trends in actual test weight (Fig. 5). The IWPN surpassed the standard cultivar early in the breeding program, but until recently, the IWPN generally had lower test weight. One disturbing trend has been a gradual decline in the mean test weight for both IWPN and standard cultivar. Also, neither the IWPN nor the standard cultivar (except in 1979 and 1980) rarely attained the target test weight of 772.2 kg m^{-3} (60 lbs bu^{-1}). The AWPN exhibited a similar trend relative to the standard cultivar as did the IWPN (Fig. 6). The AWPN exceeded the standard check cultivar for a greater number of years (9 vs. 7 years for IWPN), but the AWPN usually had lower mean test weight than the IWPN. In recent years (1991-1992), both the IWPN and AWPN have shown superiority in mean test weight over the standard cultivar, Chisholm (Fig. 7). The results for test weight clearly indicate that genetic improvement for this secondary trait has been modest; greater attention must be given in the future to counteract environmental pressure toward lower test weight.

Optimum heading date of a wheat cultivar results in good grain filling and ultimately high yield and test weight. A cultivar must be early enough to avoid periods of drought stress during anthesis due to excessive high temperatures and hot, dry winds, but late enough to escape freezing temperatures which may occur in late winter or early spring. Selection differentials and genetic gains for heading date in Phase II of the OAES wheat breeding program varied throughout the 24-year period examined (Table 6). Negative selection differentials were observed in fifteen years of the breeding program, indicating greater emphasis on early heading date. The selected lines from the IWPN consistently headed earlier than the whole population from 1982 to 1993 (except in 1986), resulting in negative selection differentials for the last decade of selection. The lowest selection differential of -10.8% of the check mean was observed at the beginning (1969) of the breeding program. Many of the parents used in the breeding program prior to that time were closely related to, or possibly direct descendants of the late maturing cultivar, Turkey. The experimental lines selected for earliness in the IWPN mostly had early heading date in the following year's AWPN, resulting in negative genetic gains. The lowest desirable genetic gain of -11.5% of the check mean was noticed as late as 1991-1992.

Based on the 3-year moving mean for days to heading, the IWPN was earlier in heading than the standard cultivar for many years in the beginning of the breeding program (Fig. 8). In 1979 and early 1980s, both the IWPN and AWPN as well as the corresponding standard cultivar exhibited relatively late heading (Fig. 8 and 9). But interestingly, almost in the same period the 3-year average grain yield of the three nurseries, as well as the corresponding standard cultivars, was maximum. Since 1984, both the IWPN and AWPN have had later heading dates than the standard cultivar, Chisholm (Fig. 10). In most years the experimental lines in the AWPN required fewer days (as a percent of the standard cultivar) to heading than the IWPN.

The data may be summarized by determining average selection differential and genetic gain for grain yield, test weight, and heading date across the 24-year period (Table 7). As a percentage of the common checks, mean selection differential for grain yield was 4.3 percentage units greater in Phase I than Phase II, but the mean genetic gain for grain yield was about the same in Phases I and II of the breeding program (Table 7). Schmidt (1984) reported an annual rate of genetic gain of 0.74% for the period, 1958 to 1980, based on data from uniform regional performance nurseries. Cox et al. (1988) reported a per-annum genetic gain of 0.6% by evaluating wheat cultivars from different breeding eras in a common environment.

The regression coefficient for genetic gain vs. selection differential, an estimate of realized heritability, was slightly lower (0.35) in Phase I than in Phase II (0.51) for grain yield. Based on their standard errors, these estimates were not statistically different. A higher heritability might be expected in Phase II because fewer lines were evaluated in more replications and locations than in Phase I. Sidwell et al. (1976) and Teich (1984) also reported intermediate broad-sense heritabilities (0.36 and 0.30, respectively) for yield from F_2 and backcross populations in wheat. Almost similar estimates for selection differential, genetic gain and realized heritability were obtained by St. Martin and McBlain (1991) in a similar study conducted in soybean.

As expected for a secondary selection trait, the mean selection differential for test weight was only 0.7% of the common check mean (Table 7). The mean genetic gain and regression coefficient were also low (0.2% and 0.33, respectively) for test weight in Phase II of the breeding program. Cox et al. (1988) observed an increase of 0.4 kg m^{-3} yr^{-1} in test weight for hard red winter wheat by regressing cultivar mean on year of release for the period of 1874 to 1987. While reports of heritabilities for test weight are limited in the literature, Ghaderi and Everson (1971) and Teich (1984) have reported high heritability

(0.94 and 0.98, respectively) for test weight in wheat, indicating that improvement is possible for this trait. Genetic gains for test weight in Phase II were highly variable from year to year, resulting in a large standard error and a nonsignificant G value.

Mean selection differential was negative for heading date, indicating that the experimental lines tested in Phase II of the breeding program were generally earlier than the common check cultivar. However, the average genetic gain for heading date was not significant, as genetic gains for heading date were variable from year to year. Cox et al. (1988) estimated that days to heading have decreased at a rate of -0.1 d yr^{-1} during the period 1874 to 1987. As reported by others (Johnson et al., 1966; Anwar and Chowdhry, 1969; and Ketata et al., 1976) realized heritability was high for heading date (0.75) in Phase II. Desirable earliness can be achieved through selection, but as in the case for test weight, selection has thus far been inconsistent in direction (positive vs. negative) to allow significant overall gains. This inconsistency likely reflects breeder preference for a "window" of desirable maturity dates rather than an inability to select unidirectionally for maturity.

CHAPTER V

SUMMARY AND CONCLUSIONS

Genetic improvement has played a major role in yield gains in Oklahoma's past and undoubtedly will be important in its future. The OAES wheat breeding program has been successful in improving yield potential by > 4% per year and in releasing new cultivars in the past 24 years. The realized heritabilities estimated for grain yield indicate the effectiveness of selection in various testing phases of the breeding program. Multi-location testing of the nurseries has been very effective in generating elite lines for release as improved cultivars or germplasms. Over the 24-year period, nine wheat cultivars (Agent, Danne, Nicoma, Osage, Payne, Chisholm, Century, and Cimarron) and numerous high quality germplasm lines have been released from the breeding program. These are used as parents in wheat breeding programs throughout the world.

Though expensive in terms of labor and time, experimental lines should be evaluated for secondary traits (e.g., test weight) in the early stages (PYN and IWPN) of multi-location testing. Trends in average yield performance are encouraging because for the last decade, the IWPN and AWPN have almost consistently out-yielded the standard cultivar, Chisholm, which occupied almost one-third of Oklahoma's wheat acreage as recently as 1991. However, genetic gains for test weight have been modest, which indicates a lower emphasis for that trait and/or the difficulty in improving grain yield and test weight simultaneously. Being a standard for wheat marketing and prices, genetic improvement in test weight requires more consideration in the breeding program. It has been demonstrated recently that recurrent selection is a very effective breeding procedure for improving test weight and grain yield simultaneously in oat (Klein et al., 1993). Recurrent selection can contribute to cultivar development if integrated with conventional pedigree breeding methods (Carver and Bruns, 1993). Emphasis should be placed on elite germplasms or cultivars as parents which have known superiority for both grain yield and test weight, accompanied by appropriate heading date. Even then, the extent to which these gains are reflected in released cultivars will be influenced by other selection pressures, such as end-use quality and pest resistance.

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TABLE 1

NUMBER OF LINES TESTED AND SELECTED PER YEAR IN THE PRELIMINARY YIELD NURSERY (PYN) AND INTERMEDIATE WHEAT PERFORMANCE NURSERY (IWPN) OF THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1992.

	PYN			IWPN		
Harvest year	Lines tested	Lines selected[a]	Proportion selected	Lines tested	Lines selected[b]	Proportion selected
	--- no. ---		%	--- no. ---		%
1992	200	30	15.0	33	20	60.6
1991	200	7	3.5	25	4	16.0
1990	200	25	12.5	24	6	25.0
1989	175	22	12.6	24	11	45.8
1988	175	22	12.6	33	12	36.4
1987	175	27	15.4	34	9	26.5
1986	200	34	17.0	34	10	29.4
1985	200	31	15.5	34	10	29.4
1984	275	30	10.9	50	11	22.0
1983	275	38	13.8	50	11	22.0
1982	275	50	18.2	50	9	18.0
1981	350	50	14.3	25	8	32.0
1980	250	25	10.0	25	10	40.0
1979	100	25	25.0	25	10	40.0
1978	154	23	14.9	25	6	24.0
1977	200	24	12.0	25	8	32.0
1976	200	24	12.0	25	14	56.0
1975	125	20	16.0	25	7	28.0
1974	125	21	16.8	25	7	28.0
1973	125	22	17.6	25	10	40.0
1972	100	23	23.0	25	7	28.0
1971	75	19	25.3	25	10	40.0
1970	71	14	19.7	21	2	9.5
1969	56	12	21.4	19	3	15.8

[a]To be tested the following year in the IWPN

[b]To be tested the following year in the AWPN

TABLE 2

ILLUSTRATION OF PROCEDURE TO ESTIMATE SELECTION DIFFERENTIAL (I) AND GENETIC GAIN (G) FOR GRAIN YIELD IN PHASE I (PYN TO IWPN) AND PHASE II (IWPN TO AWPN) IN THE OAES WHEAT BREEDING PROGRAM.

				Grain yield	
Phase	Year	Nursery	Statistic	Actual	% of Check
				kg ha^{-1}	%
I[a]	1991	PYN	$\bar{X}$	2711.1	93.1
			$\bar{X}_s$	2985.9	102.5
			$\bar{X}_c$	2913.4	100.0
			I	274.8	9.4
	1992	IWPN	$\bar{X}'_s$	3446.2	105.1
			$\bar{X}'_c$	3277.5	100.0
			G	371.0	12.0
II[b]	1992	IWPN	$\bar{X}$	3726.4	113.6
			$\bar{X}_s$	3923.2	119.6
			$\bar{X}_c$	3281.6	100.0
			I	196.8	6.0
	1993	AWPN	$\bar{X}'_s$	3218.4	110.1
			$\bar{X}'_c$	2922.8	100.0
			G	-149.2	-3.5

[a]Phase I: $\bar{X}$ = mean of 200 lines; $\bar{X}_s$ = mean of seven selections; $\bar{X}_c$ = mean of five common checks (Chisholm, Mesa, Karl, TAM 200, and 2180); $\bar{X}'_s$ = mean of seven selections the following year; $\bar{X}'_c$ = mean of five common checks the following year (same as for $\bar{X}_c$ in Phase I).

[b]Phase II: $\bar{X}$ = mean of 33 lines; $\bar{X}_s$ = mean of 20 selections; $\bar{X}_c$ = mean of seven common checks (Chisholm, Mesa, Karl, TAM 200, Cimarron, 2163 and 2180); $\bar{X}'_s$ = mean of 20 selections the following year; $\bar{X}'_c$ = mean of seven common checks the following year (same as for $\bar{X}_c$ in Phase II).

TABLE 3

MEANS[a] FOR GRAIN YIELD (AS A PERCENTAGE OF THE CHECK) OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE I NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	PYN		IWPN		
(PYN-IWPN)	$\bar{X}$	$\bar{X}_s$	$\bar{X}'_s$	I	G
	%				
1992-93	101.9	124.0	101.5	22.1	-0.4
1991-92	93.1	102.5	105.1	9.4	12.0
1990-91	99.9	112.3	92.7	12.4	-7.2
1989-90	91.7	100.0	94.9	8.3	3.2
1988-89	94.5	103.9	100.8	9.4	6.3
1987-88	95.7	106.1	108.6	10.4	12.9
1986-87	101.4	109.2	107.7	7.8	6.3
1985-86	112.3	118.0	109.8	5.7	-2.5
1984-85	98.5	106.8	109.1	8.3	10.6
1983-84	96.6	111.6	100.2	15.0	3.6
1982-83	98.0	110.9	105.1	12.9	7.1
1981-82	96.7	112.5	99.3	15.8	2.6
1980-81	93.7	109.4	94.8	15.7	1.1
1979-80	97.1	104.9	98.8	7.8	1.7
1978-79	90.0	104.7	94.5	14.7	4.5
1977-78	90.1	105.5	101.2	15.4	11.1
1976-77	92.1	108.4	100.5	16.3	8.4
1975-76	103.6	114.9	102.9	11.3	-0.7
1974-75	88.3	99.8	100.7	11.5	12.4
1973-74	94.1	103.9	91.2	9.8	-2.9
1972-73	89.4	105.3	97.3	15.9	7.9
1971-72	92.9	99.9	102.0	7.0	9.1
1970-71	92.5	107.6	98.9	15.1	6.4
1969-70	101.2	110.1	99.2	8.9	-2.0

[a]$\bar{X}$ = mean of all experimental lines in PYN as % of common checks.

$\bar{X}_s$ = mean of selected lines in PYN as % of common checks.

$\bar{X}'_s$ = mean of lines selected from PYN and tested in IWPN the following year as % of common checks.

I = selection differential.

G = genetic gain.

TABLE 4

MEANS[a] FOR GRAIN YIELD (AS A PERCENTAGE OF THE CHECK) OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE II NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	IWPN		AWPN		
(IWPN-AWPN)	$\bar{X}$	$\bar{X}_s$	$\bar{X}'_s$	I	G
	%				
1992-93	113.6	119.6	110.1	6.0	-3.5
1991-92	92.7	99.5	113.7	6.8	21.0
1990-91	95.9	104.2	100.0	8.3	4.1
1989-90	100.0	106.4	104.2	6.4	4.2
1988-89	105.2	110.2	99.7	5.0	-5.5
1987-88	107.5	113.5	111.4	6.0	3.9
1986-87	102.6	112.1	100.9	9.5	-1.7
1985-86	104.3	115.0	106.9	10.7	2.6
1984-85	101.1	107.6	109.2	6.5	8.1
1983-84	104.7	111.0	101.7	6.3	-3.0
1982-83	101.5	108.3	110.7	6.8	9.2
1981-82	94.8	104.9	102.7	10.1	7.9
1980-81	100.2	104.1	104.4	3.9	4.2
1979-80	100.5	104.8	99.7	4.3	-0.8
1978-79	99.6	105.2	103.2	5.6	3.6
1977-78	99.9	104.1	103.9	4.2	4.0
1976-77	95.3	100.7	98.1	5.4	2.8
1975-76	105.9	114.9	104.6	9.0	-1.3
1974-75	89.8	99.0	105.1	9.2	15.3
1973-74	98.6	108.7	104.9	10.1	6.3
1972-73	98.7	111.9	96.7	13.2	-2.0
1971-72	94.8	102.2	100.7	7.4	5.9
1970-71	95.2	107.5	93.8	12.3	-1.4
1969-70	91.5	103.9	107.1	12.4	15.6

[a]$\bar{X}$ = mean of all experimental lines in IWPN as % of common checks.

$\bar{X}_s$ = mean of selected lines in IWPN as % of common checks.

$\bar{X}'_s$ = mean of lines selected from IWPN and tested in AWPN the following year as % of common checks.

I = selection differential.

G = genetic gain.

TABLE 5

MEANS[a] FOR TEST WEIGHT (AS A PERCENTAGE OF THE CHECK) OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE II NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	IWPN		AWPN		
(IWPN-AWPN)	$\bar{X}$	$\bar{X}_s$	$\bar{X}'_s$	I	G
	%				
1992-93	102.2	103.0	100.8	0.8	-1.4
1991-92	99.2	99.9	99.1	0.7	-0.1
1990-91	98.5	100.0	99.2	1.5	0.7
1989-90	100.8	101.1	99.9	0.3	-0.9
1988-89	100.5	100.8	101.0	0.3	0.5
1987-88	100.8	102.6	102.0	1.8	1.2
1986-87	100.4	101.0	100.9	0.6	0.5
1985-86	101.5	103.4	102.2	1.9	0.7
1984-85	99.8	99.7	99.7	-0.1	-0.1
1983-84	101.2	101.9	101.0	0.7	-0.1
1982-83	99.5	99.7	100.4	0.2	0.9
1981-82	100.0	100.4	100.1	0.4	0.1
1980-81	99.8	100.5	101.8	0.7	2.0
1979-80	99.1	99.0	98.0	-0.1	-1.1
1978-79	99.9	99.6	98.8	-0.3	-1.1
1977-78	100.0	100.8	99.3	0.8	-0.7
1976-77	99.7	100.0	99.0	0.3	-0.7
1975-76	101.1	101.8	100.9	0.7	-0.2
1974-75	99.2	99.9	100.7	0.7	1.5
1973-74	99.3	99.8	99.3	0.5	0.0
1972-73	100.0	100.3	100.2	0.3	0.2
1971-72	101.1	101.5	101.2	0.4	0.1
1970-71	101.1	103.9	101.5	2.8	0.4
1969-70	100.9	101.8	102.0	0.9	1.1

[a]$\bar{X}$ = mean of all experimental lines in IWPN as % of common checks.

$\bar{X}_s$ = mean of selected lines in IWPN as % of common checks.

$\bar{X}'_s$ = mean of lines selected from IWPN and tested in AWPN the following year as % of common checks.

I = selection differential.

G = genetic gain.

TABLE 6

MEANS[a] FOR HEADING DATE (AS A PERCENTAGE OF THE CHECK) OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE II NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	IWPN		AWPN		
(IWPN-AWPN)	$\bar{X}$	$\bar{X}_s$	$\bar{X}'_s$	I	G
	--------------------	--------------------	%	--------------------	--------------------
1992-93	95.3	94.9	99.9	-0.4	4.6
1991-92	113.8	108.7	102.3	-5.1	-11.5
1990-91	107.1	104.9	112.5	-2.2	5.4
1989-90	100.3	97.8	103.3	-2.5	3.0
1988-89	95.9	94.1	91.1	-1.8	-4.8
1987-88	98.3	94.9	97.3	-3.4	-1.0
1986-87	89.7	96.2	98.1	6.5	8.4
1985-86	102.9	100.5	99.8	-2.4	-3.1
1984-85	100.1	98.7	96.1	-1.4	-4.0
1983-84	99.1	96.2	98.6	-2.9	-0.5
1982-83	105.7	100.3	103.4	-5.4	-2.3
1981-82	102.1	103.9	102.5	1.8	0.4
1980-81	101.1	103.2	100.0	2.1	-1.1
1979-80	101.2	101.4	104.4	0.2	3.2
1978-79	98.0	103.0	100.0	5.0	2.4
1977-78	104.2	97.2	98.1	-7.0	-6.1
1976-77	97.5	97.4	93.9	-0.1	-3.6
1975-76	97.5	97.8	88.7	0.3	-8.8
1974-75	93.6	94.1	98.6	0.5	5.0
1973-74	100.6	99.1	98.4	-1.5	-2.2
1972-73	96.5	97.1	99.6	0.6	3.1
1971-72	106.9	107.6	108.0	0.7	1.1
1970-71	101.5	97.5	99.6	-4.0	-1.9
1969-70	99.3	88.5	92.8	-10.8	-6.5

[a]$\bar{X}$ = mean of all experimental lines in IWPN as % of common checks.

$\bar{X}_s$ = mean of selected lines in IWPN as % of common checks.

$\bar{X}'_s$ = mean of lines selected from IWPN and tested in AWPN the following year as % of common checks.

I = selection differential.

G = genetic gain.

TABLE 7

MEAN SELECTION DIFFERENTIAL (I), GENETIC GAIN (G), AND COEFFICIENT OF REGRESSION OF (H) G ON I FOR GRAIN YIELD, TEST WEIGHT, AND HEADING DATE FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

	Phase I (PYN to IWPN)			Phase II (IWPN to AWPN)		
Trait	I	G	H	I	G	H
	% of checks			% of checks		
Grain yield	12.0	4.6	0.35	7.7	4.2	0.51
SE	0.8	1.1	0.09	0.6	1.3	0.16
Test weight	—	—	—	0.7	0.2	0.33
SE	—	—	—	0.1	0.2	0.17
Heading date	—	—	—	-1.4	-0.9	0.75
SE	—	—	—	0.8	1.0	0.20

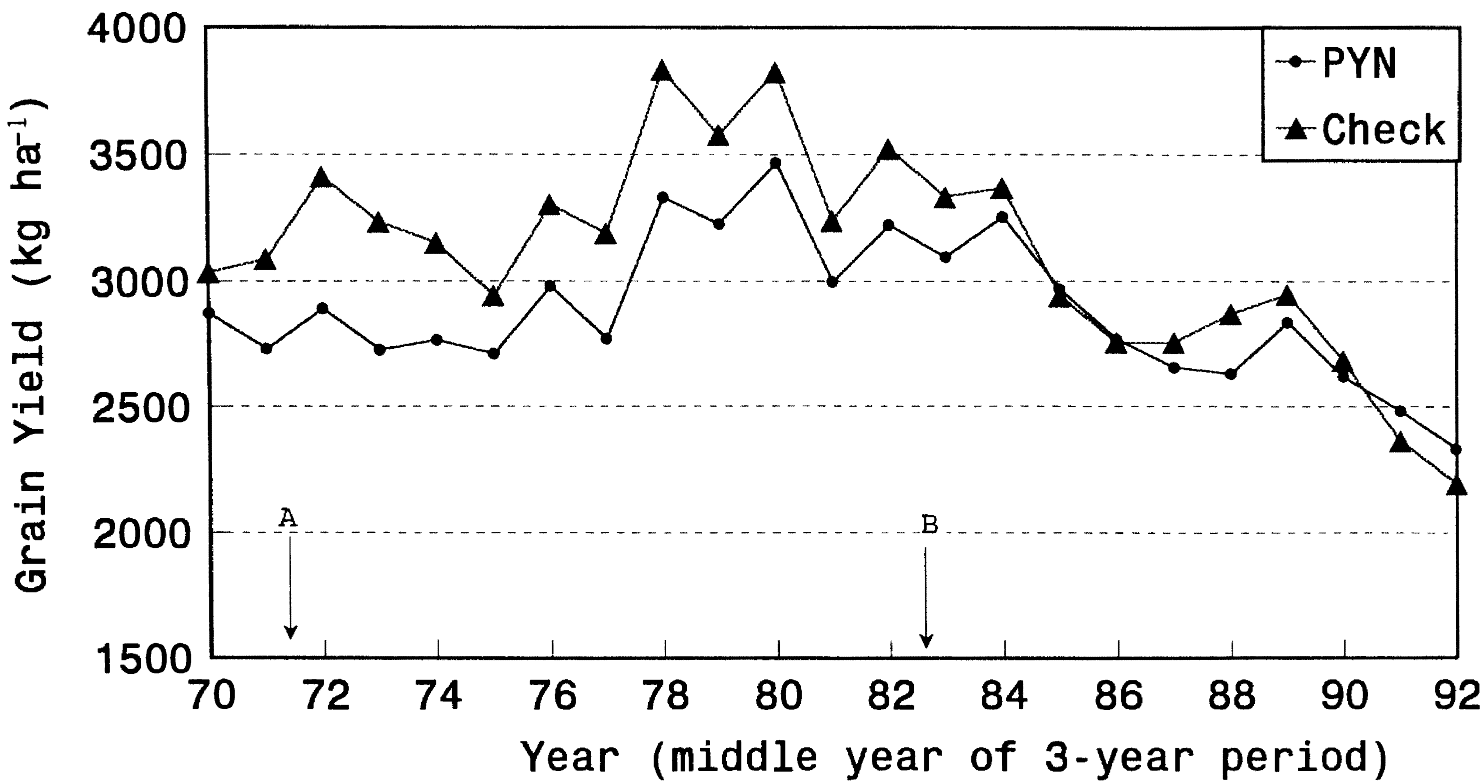

Figure 1. Three-Year Moving Average for Grain Yields of the PYN and Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

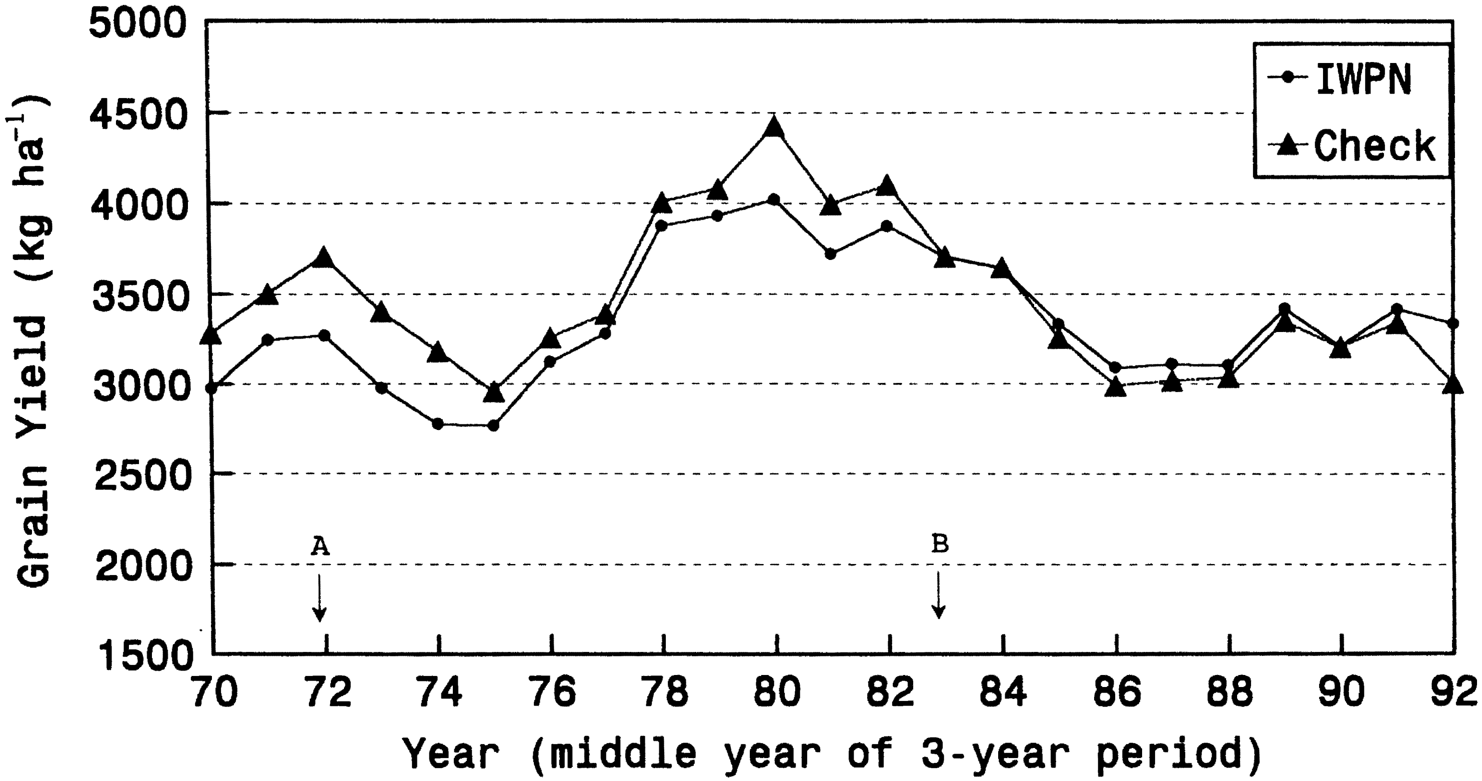

Figure 2. Three-Year Moving Average for Grain Yields of the IWPN and Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

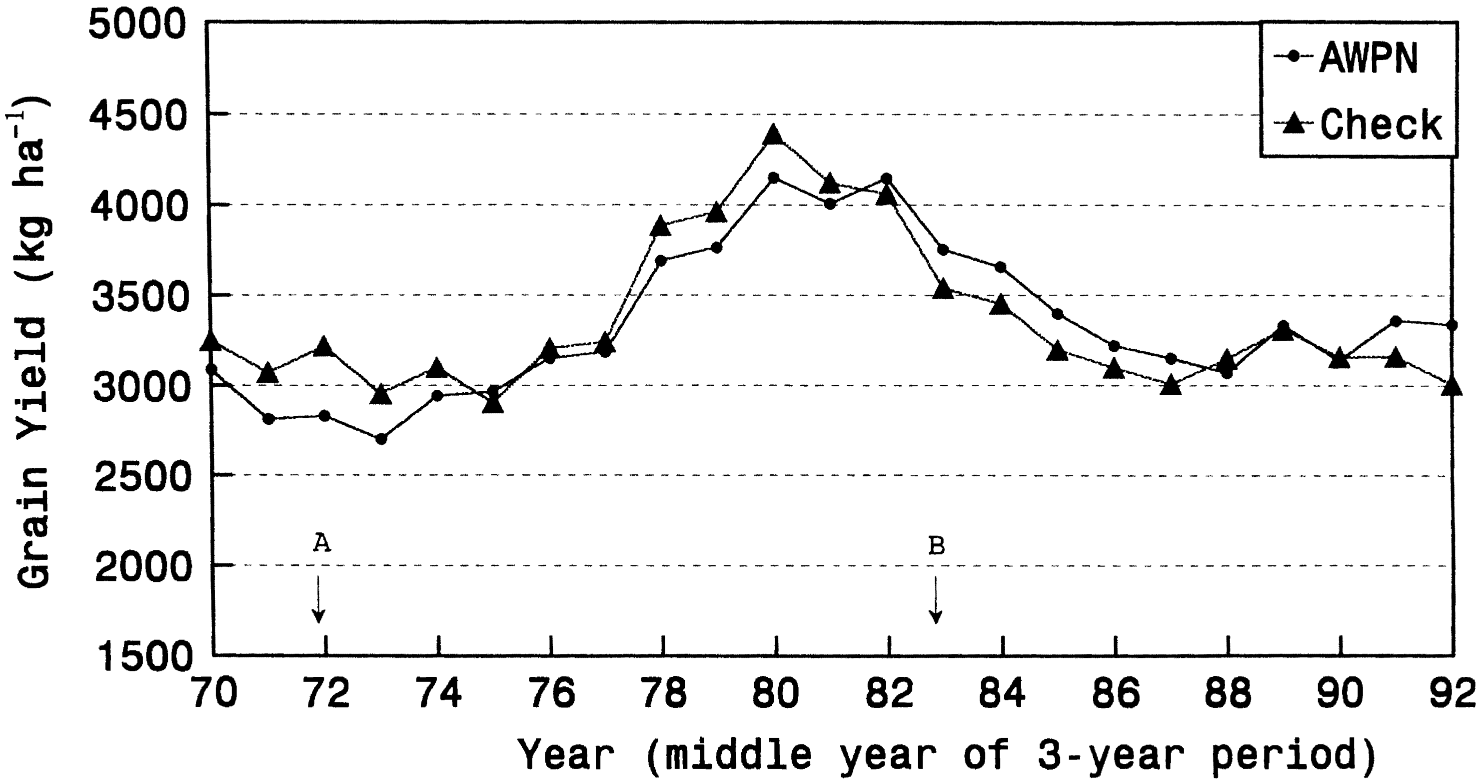

Figure 3. Three-Year Moving Average for Grain Yields of the AWPN and Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

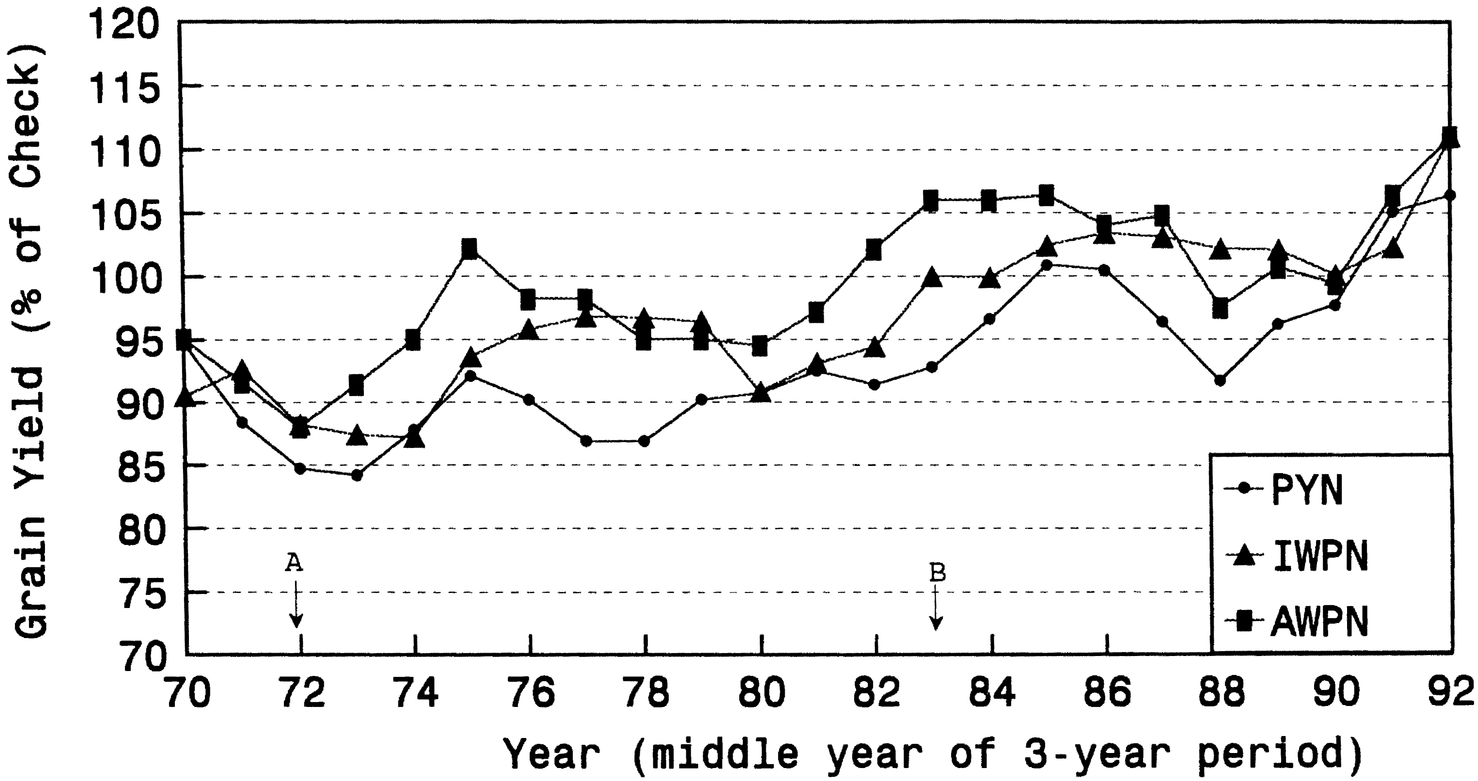

Figure 4. Three-Year Moving Average for Grain Yields of the PYN, IWPN, and AWPN Expressed as Percentages of the Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

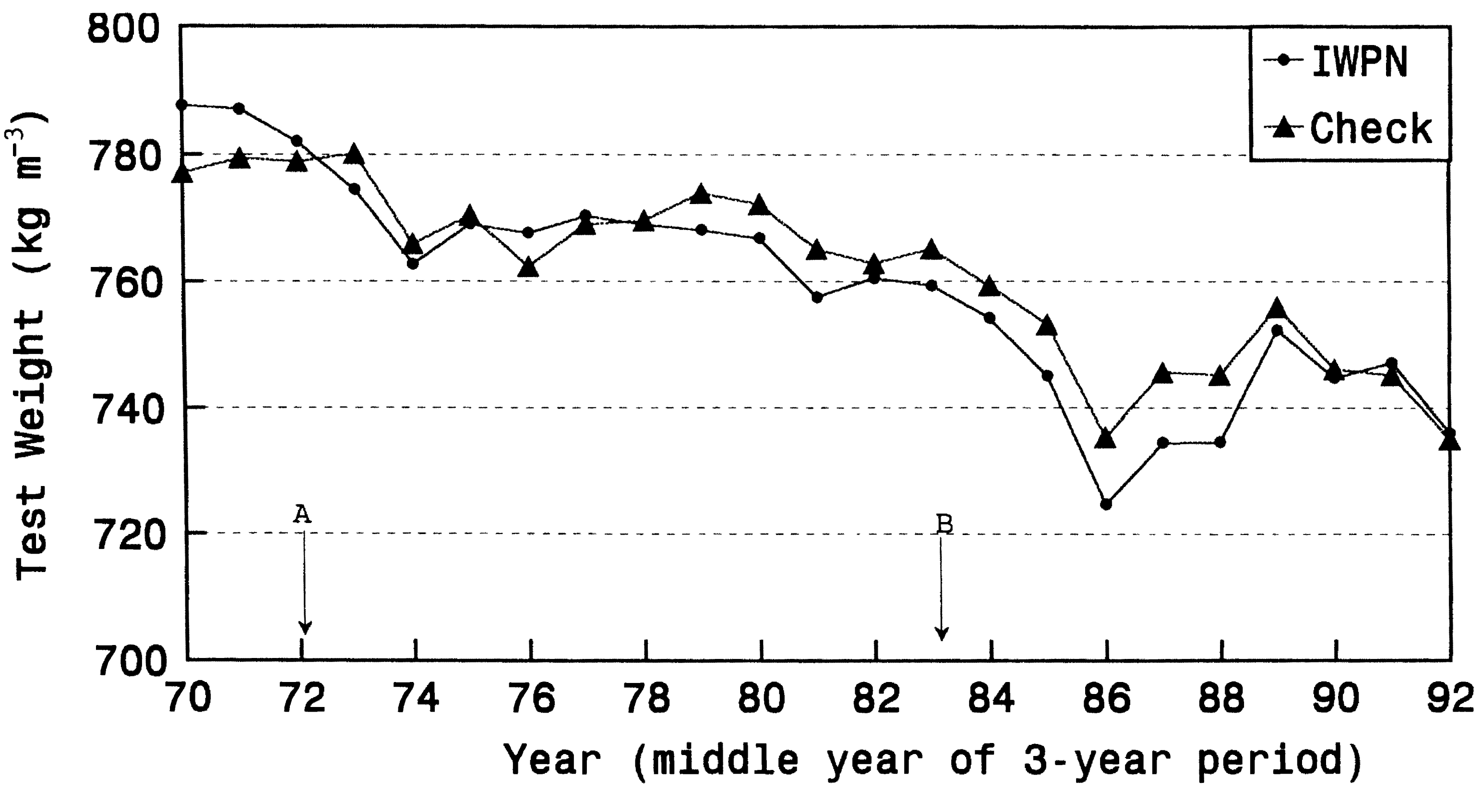

Figure 5. Three-Year Moving Average for Test Weights of the IWPN and Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

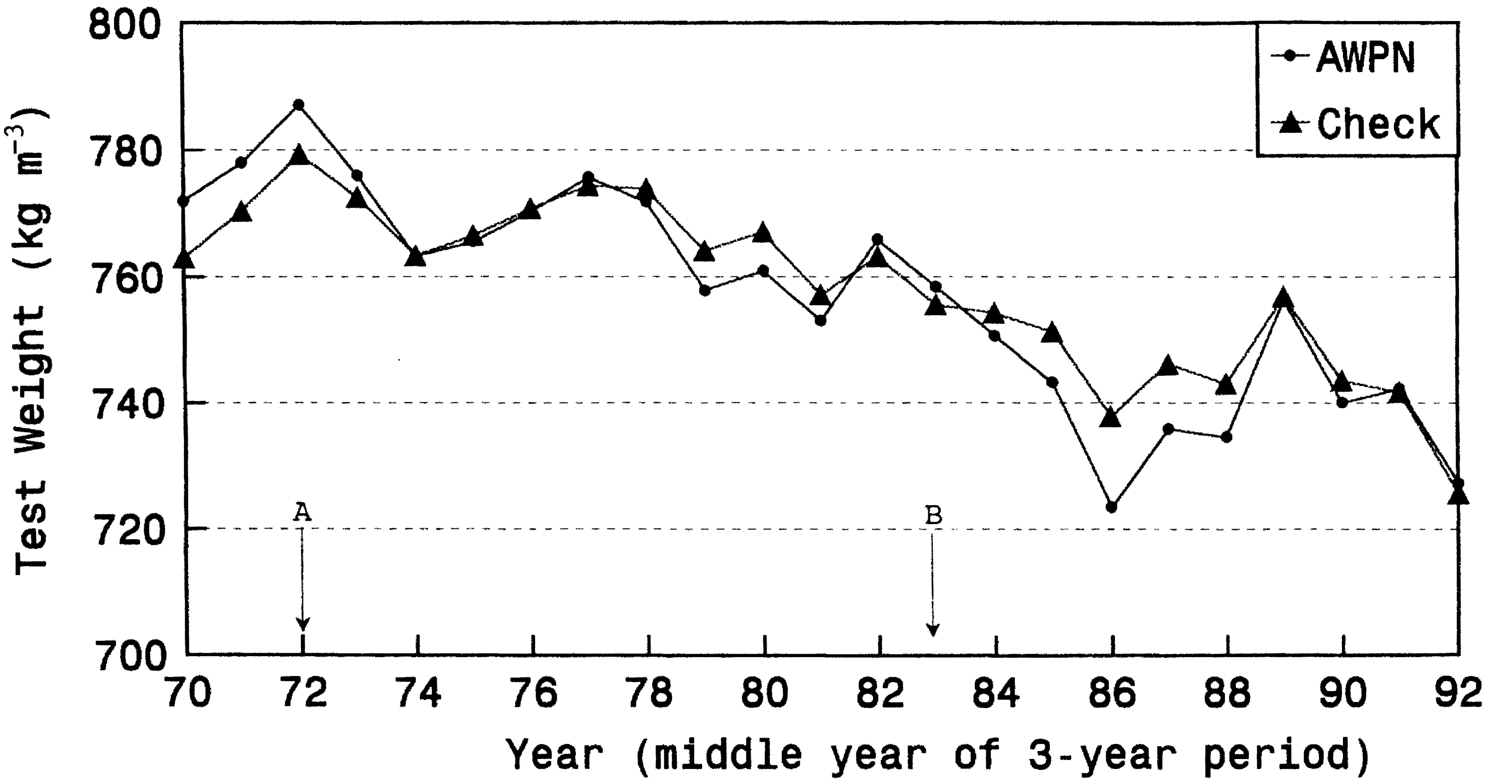

Figure 6. Three-Year Moving Average for Test Weights of the AWPN and Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

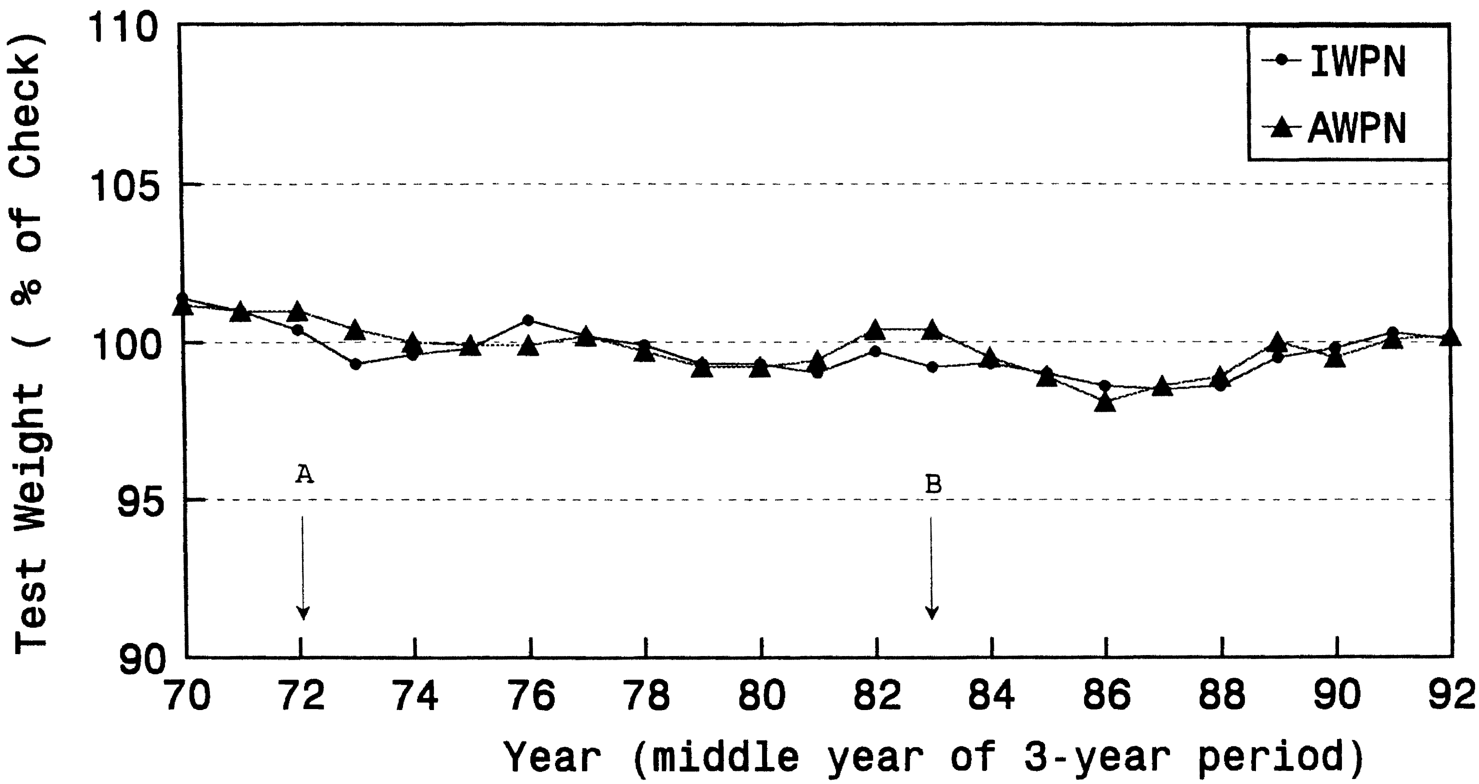

Figure 7. Three-Year Moving Average for Test Weights of the IWPN and AWPN Expressed as Percentages of the Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

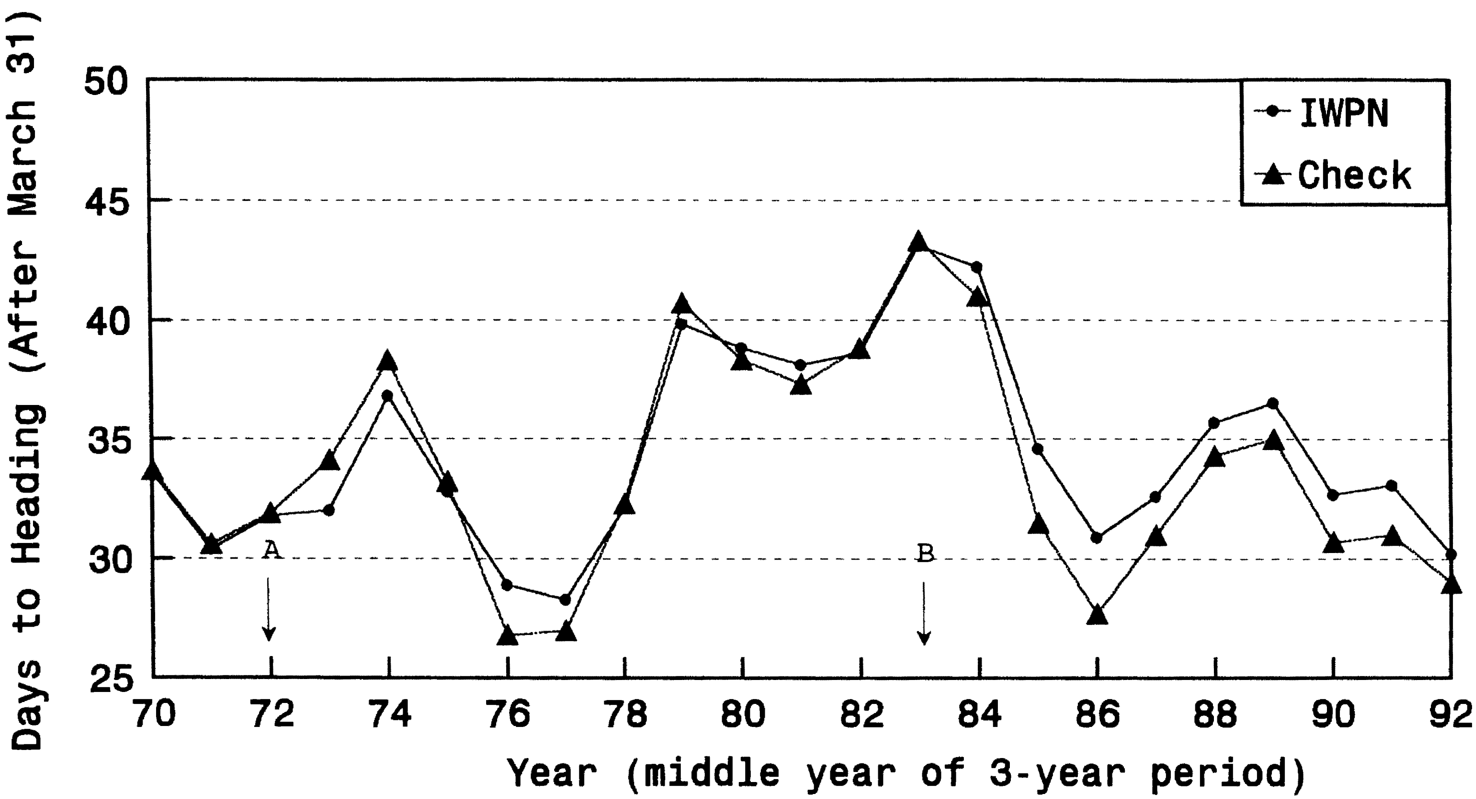

Figure 8. Three-Year Moving Average for Days to Heading of the IWPN and Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

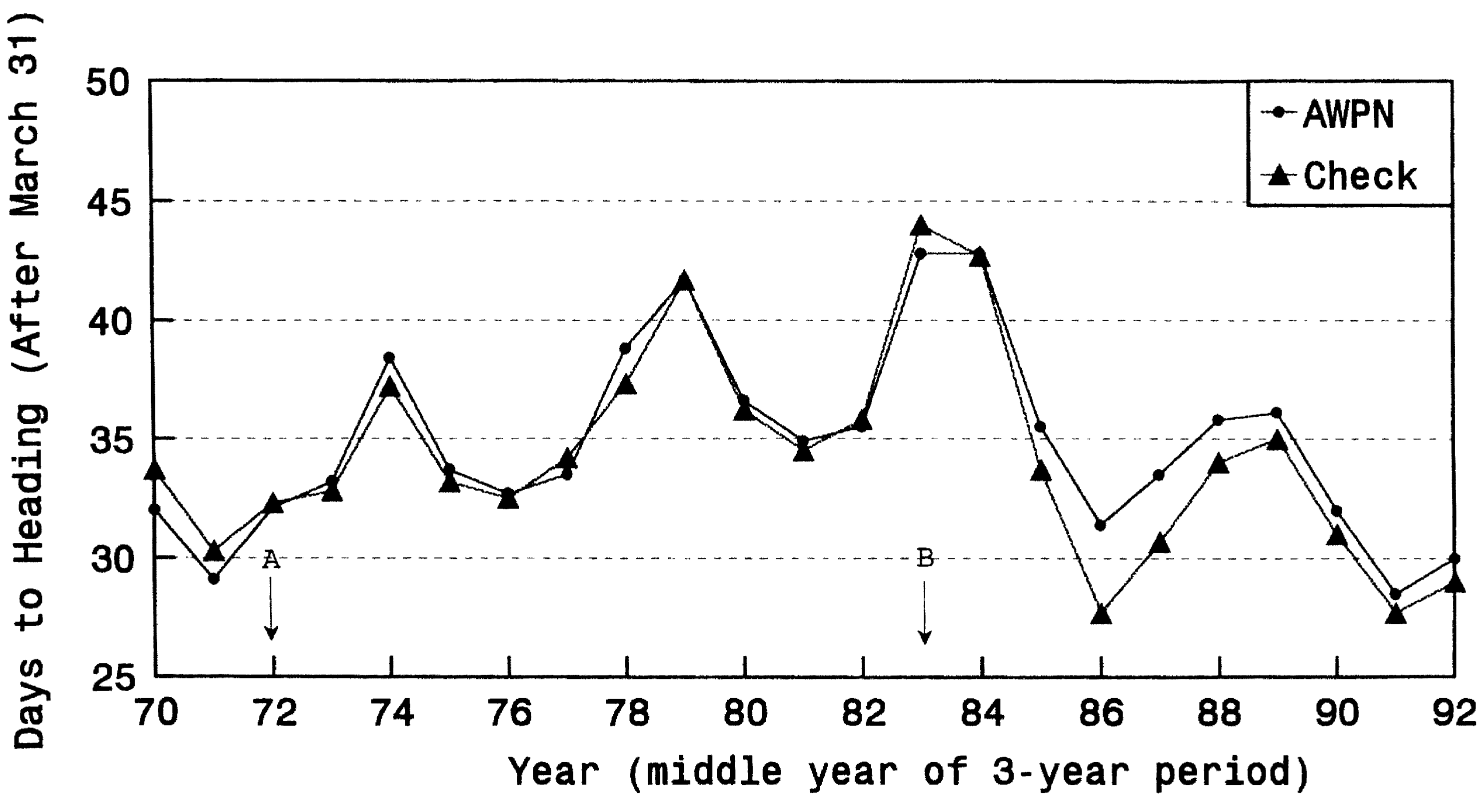

Figure 9. Three-Year Moving Average for Days to Heading of the AWPN and Standard Check Cultivar in the OAES Wheat Breeding Program, 1969 to 1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

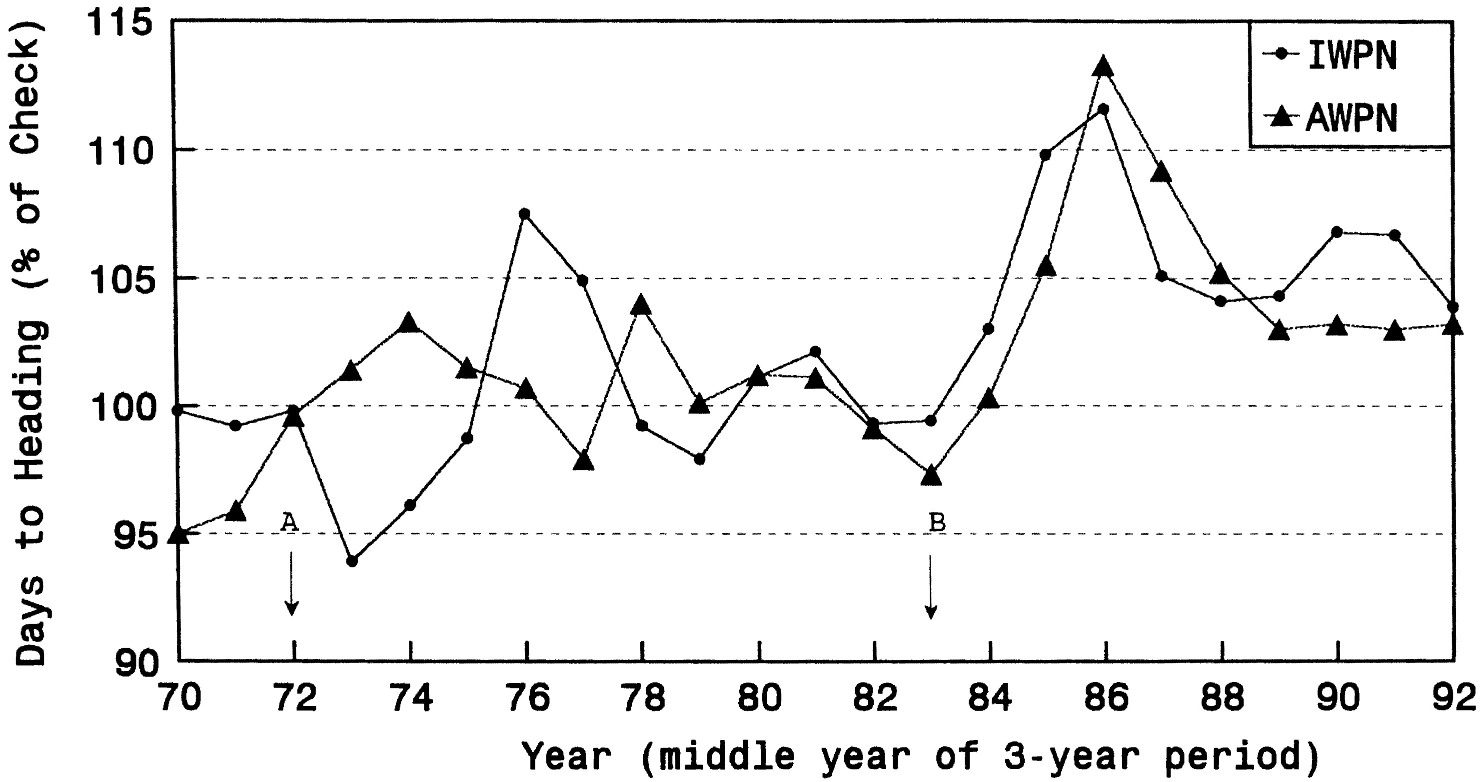

Figure 10. Three-Year Moving Average for Days to Heading of the IWPN and AWPN Expressed as Percentages of the Long-Term Check in the OAES Wheat Breeding Program, 1969-1993.

Arrows A and B indicate change in check from Scout 66 to TAM W-101, and from TAM W-101 to Chisholm (with Payne in 1982), respectively.

APPENDIX

SUPPLEMENTAL DATA FOR

TABLES 3-7, AND FIGURES 1-10

TABLE 1

MEANS[a] FOR GRAIN YIELD OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE I NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	PYN			IWPN			
(PYN-IWPN)	$\bar{X}$	$\bar{X}_s$	$\bar{X}_c$	$\bar{X}'_s$	$\bar{X}'_c$	I	G
	kg ha^{-1}						
1992-93	1954.6	2379.2	1918.9	3180.8	3135.1	424.6	10.1
1991-92	2711.1	2985.9	2913.4	3446.2	3277.5	274.8	370.9
1990-91	2785.7	3131.0	2788.4	3127.0	3372.9	345.3	-243.2
1989-90	2360.4	2572.0	2572.7	3375.6	3556.4	211.6	31.6
1988-89	3358.2	3694.8	3555.0	3082.7	3059.2	336.6	220.4
1987-88	2175.6	2411.4	2273.0	3742.5	3444.8	235.8	395.1
1986-87	2432.3	2619.7	2398.7	2449.7	2274.4	187.4	141.9
1985-86	3697.5	3883.6	3292.3	3143.8	2864.3	186.1	-125.7
1984-85	2772.9	3006.1	2814.6	3753.9	3442.1	233.2	353.5
1983-84	3291.6	3805.0	3408.5	3219.1	3213.7	513.4	122.3
1982-83	3216.4	3638.3	3280.2	4054.9	3859.4	421.9	259.3
1981-82	3153.9	3668.6	3262.1	3798.2	3824.4	514.7	82.0
1980-81	2617.7	3055.8	2792.4	3691.4	3894.3	438.1	-28.2
1979-80	4634.1	5001.6	4769.8	3586.6	3628.3	367.5	94.0
1978-79	2428.9	2823.3	2697.7	4795.3	5072.8	394.4	-8.7
1977-78	2930.2	3432.1	3252.7	3426.7	3385.0	501.9	364.2
1976-77	2952.3	3477.7	3207.0	3413.2	3395.1	525.4	272.8
1975-76	3055.1	3386.4	2947.6	3031.6	2944.9	331.3	-20.8
1974-75	2123.9	2398.7	2404.1	2914.0	2892.5	274.8	301.7
1973-74	3116.9	3441.5	3313.1	2393.3	2625.1	324.6	-35.6
1972-73	2932.2	3454.2	3280.9	3067.2	3151.2	522.2	264.7
1971-72	2623.1	2820.0	2823.3	3614.1	3544.3	196.9	270.0
1970-71	2635.2	3063.2	2847.5	3316.5	3354.8	428.0	174.0
1969-70	3361.5	3657.8	3321.2	3141.8	3168.0	296.3	-66.5

[a] $\bar{X}$ = mean of all experimental lines in PYN.

$\bar{X}_c$ = mean of common checks in PYN.

$\bar{X}_s$ = mean of selected lines in PYN.

$\bar{X}'_s$ = mean of lines selected in PYN and tested in IWPN next year.

$\bar{X}'_c$ = mean of common checks in IWPN.

I = selection differential.

G = genetic gain.

TABLE 2

MEANS[a] FOR GRAIN YIELD OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE II NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	IWPN			AWPN			
(IWPN-AWPN)	$\bar{X}$	$\bar{X}_s$	$\bar{X}_c$	$\bar{X}'_s$	$\bar{X}'_c$	I	G
	---------- kg ha^{-1} ----------						
1992-93	3726.4	3923.2	3281.6	3218.4	2922.8	196.8	-149.2
1991-92	3127.0	3358.2	3374.3	3707.5	3262.1	231.2	692.7
1990-91	3392.4	3687.4	3538.2	3238.6	3237.2	295.0	147.2
1989-90	3098.8	3297.7	3099.5	3388.4	3250.6	198.9	138.5
1988-89	3758.6	3934.6	3571.1	2934.9	2944.9	176.0	-197.5
1987-88	2451.1	2586.1	2279.1	3610.1	3241.2	135.0	196.9
1986-87	3119.6	3408.5	3040.3	2512.9	2490.7	288.9	-57.1
1985-86	3692.8	4071.7	3540.9	3093.4	2894.5	378.9	47.0
1984-85	3181.4	3385.7	3147.2	3847.3	3523.4	204.3	289.7
1983-84	4052.2	4296.1	3870.8	3039.7	2988.6	243.9	-130.3
1982-83	3880.9	4140.2	3824.4	4148.3	3745.2	259.3	346.6
1981-82	3691.4	4084.5	3894.3	4087.8	3979.0	393.1	311.7
1980-81	3586.6	3728.4	3581.2	4163.8	3988.4	141.8	170.0
1979-80	4786.6	4992.9	4762.4	3586.6	3598.0	206.3	-35.6
1978-79	3422.7	3616.2	3437.4	4785.3	4637.4	193.5	162.6
1977-78	3415.9	3560.4	3418.6	3245.9	3124.3	144.5	124.3
1976-77	2995.3	3166.7	3144.5	3279.5	3344.0	171.4	84.7
1975-76	2946.9	3195.6	2781.7	3001.4	2869.0	248.7	-32.8
1974-75	2358.4	2600.3	2625.1	3174.1	3018.8	241.9	422.0
1973-74	3016.8	3326.6	3059.8	2748.1	2619.1	309.8	172.0
1972-73	3549.0	4024.0	3596.0	2934.2	3034.3	475.0	-53.1
1971-72	3237.2	3490.5	3415.3	2282.4	2266.3	253.3	194.2
1970-71	2942.2	3322.5	3090.7	3053.8	3257.4	380.3	-55.1
1969-70	2742.0	3110.9	2995.3	3102.2	2897.2	368.9	458.3

[a] $\bar{X}$ = mean of all experimental lines in IWPN.

$\bar{X}_c$ = mean of common checks in IWPN.

$\bar{X}_s$ = mean of selected lines in IWPN.

$\bar{X}'_s$ = mean of lines selected in IWPN and tested in AWPN next year.

$\bar{X}'_c$ = mean of common checks in AWPN.

I = selection differential.

G = genetic gain.

TABLE 3

MEANS[a] FOR TEST WEIGHT OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE II NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	IWPN			AWPN			
(IWPN-AWPN)	$\bar{x}$	$\bar{x}_s$	$\bar{x}_c$	$\bar{x}'_s$	$\bar{x}'_c$	I	G
	kg m^{-3}						
1992-93	749.7	755.7	733.5	718.4	712.5	6.0	-10.3
1991-92	739.5	744.9	745.4	730.8	737.2	5.4	-0.5
1990-91	752.2	763.8	763.7	720.7	726.9	11.6	5.3
1989-90	742.1	744.4	736.2	760.2	761.3	2.3	-7.0
1988-89	762.5	764.9	758.4	746.3	738.7	2.4	3.5
1987-88	699.0	711.4	693.7	765.5	750.8	12.4	9.4
1986-87	741.4	746.1	738.5	695.7	689.6	4.7	3.2
1985-86	733.2	747.2	722.4	748.9	732.9	14.0	5.2
1984-85	760.5	759.6	761.8	729.1	731.0	-0.9	-0.6
1983-84	769.1	774.6	760.4	763.8	756.0	5.5	-0.9
1982-83	748.3	749.3	751.9	770.0	767.3	1.0	6.3
1981-82	764.0	767.0	764.2	748.8	747.7	3.0	1.3
1980-81	760.5	765.6	761.6	785.3	771.2	5.1	15.2
1979-80	776.1	775.2	783.1	731.7	746.8	-0.9	-8.1
1978-79	767.8	765.8	768.6	766.8	775.8	-2.0	-8.2
1977-78	763.1	769.4	763.2	760.5	766.0	6.3	-5.4
1976-77	779.9	782.2	782.5	770.1	777.7	2.3	-5.0
1975-76	759.7	764.7	751.1	786.9	780.2	5.0	-1.9
1974-75	767.3	773.0	773.9	765.2	760.0	5.7	11.8
1973-74	761.1	764.7	766.4	757.8	763.2	3.6	-0.1
1972-73	795.0	797.4	794.8	775.4	773.6	2.4	1.6
1971-72	790.1	792.8	781.2	792.4	783.1	2.7	0.4
1970-71	775.8	797.2	767.6	800.3	788.3	21.4	3.8
1969-70	790.3	796.8	783.0	760.9	745.8	6.5	7.8

[a]$\bar{x}$ = mean of all experimental lines in IWPN.

$\bar{x}_c$ = mean of common checks in IWPN.

$\bar{x}_s$ = mean of selected lines in IWPN.

$\bar{x}'_s$ = mean of lines selected in IWPN and tested in AWPN next year.

$\bar{x}'_c$ = mean of common checks in AWPN.

I = selection differential.

G = genetic gain.

TABLE 4

MEANS[a] FOR HEADING DATE OF ALL EXPERIMENTAL LINES AND SELECTED LINES IN PHASE II NURSERIES WITH SELECTION DIFFERENTIALS AND GENETIC GAINS FROM THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Pair of Years	IWPN			AWPN			
(IWPN-AWPN)	$\bar{X}$	$\bar{X}_s$	$\bar{X}_c$	$\bar{X}'_s$	$\bar{X}'_c$	I	G
	days after March 31						
1992-93	21.6	21.6	22.7	40.1	40.1	0.0	1.1
1991-92	28.0	26.8	24.6	22.5	22.0	-1.2	-2.9
1990-91	38.1	37.3	35.6	27.7	24.6	-0.8	0.6
1989-90	32.1	31.3	32.0	36.4	35.3	-0.8	1.0
1988-89	39.3	38.6	41.0	31.4	34.5	-0.7	-1.4
1987-88	35.8	34.6	36.4	39.9	41.0	-1.2	-0.5
1986-87	22.7	24.3	25.3	35.3	36.0	1.6	1.9
1985-86	34.2	33.4	33.3	24.7	24.8	-0.8	-1.0
1984-85	46.8	46.2	46.8	32.1	33.4	-0.6	-1.3
1983-84	45.6	44.3	46.0	46.9	47.6	-1.3	-0.3
1982-83	36.8	34.9	34.8	47.8	46.2	-1.9	-0.4
1981-82	33.3	33.9	32.6	33.6	32.8	0.6	0.1
1980-81	44.3	45.2	43.8	26.0	26.0	0.9	-0.5
1979-80	38.7	38.8	38.3	45.4	43.5	0.1	1.5
1978-79	36.4	38.3	37.2	40.2	40.0	1.9	1.0
1977-78	21.0	19.6	20.2	41.4	42.2	-1.4	-1.6
1976-77	27.5	27.4	28.2	29.4	31.3	-0.1	-1.2
1975-76	38.0	38.1	39.0	26.7	30.1	0.1	-2.4
1974-75	32.8	32.9	35.0	38.1	38.7	0.1	1.6
1973-74	39.7	39.2	39.5	32.9	33.4	-0.5	-0.7
1972-73	23.5	23.6	24.3	41.8	41.9	0.1	0.7
1971-72	32.3	32.5	30.2	23.9	22.1	0.2	-0.3
1970-71	35.4	34.0	34.9	31.3	31.4	-1.4	-0.6
1969-70	33.1	29.5	33.4	33.3	35.8	-3.6	-2.2

[a]$\bar{X}$ = mean of all experimental lines in IWPN.

$\bar{X}_c$ = mean of common checks in IWPN.

$\bar{X}_s$ = mean of selected lines in IWPN.

$\bar{X}'_s$ = mean of lines selected in IWPN and tested in AWPN next year.

$\bar{X}'_c$ = mean of common checks in AWPN.

I = selection differential.

G = genetic gain.

TABLE 5

THREE-YEAR MOVING AVERAGE FOR GRAIN YIELD OF THE PRELIMINARY YIELD NURSERY (PYN) AND STANDARD CULTIVAR IN THE OAES WHEAT BREEDING PROGRAM,1969 TO 1993.

Harvest Year	Three-Year Moving Average for Grain Yield PYN	Standard	PYN
	--------- kg ha^{-1} -------		% of Standard
1970	2873.0	3033.6	94.7
1971	2729.9	3087.4	88.4
1972	2890.5	3413.3	84.7
1973	2724.6	3234.5	84.2
1974	2765.5	3151.2	87.8
1975	2710.4	2941.6	92.1
1976	2979.2	3303.1	90.2
1977	2770.2	3188.8	86.9
1978	3331.3	3833.9	86.9
1979	3227.1	3577.2	90.2
1980	3468.4	3825.8	90.7
1981	2996.0	3238.6	92.5
1982	3220.4	3522.8	91.4
1983	3093.4	3332.6	92.8
1984	3254.0	3369.6	96.6
1985	2967.8	2940.2	100.9
1986	2768.2	2754.8	100.5
1987	2655.4	2755.5	96.4
1988	2631.2	2871.0	91.7
1989	2834.8	2947.6	96.2
1990	2619.1	2681.6	97.7
1991	2484.0	2364.4	105.1
1992	2332.8	2193.1	106.4

TABLE 6

THREE-YEAR MOVING AVERAGE FOR GRAIN YIELD OF THE INTERMEDIATE WHEAT PERFORMANCE NURSERY (IWPN) AND STANDARD CULTIVAR IN THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Harvest Year	Three-Year Moving Average for Grain Yield		
	IWPN	Standard	IWPN
	--------- kg ha^{-1} -------		% of Standard
1970	2973.8	3287.6	90.5
1971	3242.6	3500.6	92.6
1972	3267.5	3706.9	88.2
1973	2974.5	3401.8	87.4
1974	2774.3	3180.1	87.2
1975	2766.9	2956.4	93.6
1976	3119.6	3256.7	95.8
1977	3278.2	3388.4	96.8
1978	3874.9	4006.5	96.7
1979	3932.0	4080.5	96.4
1980	4021.3	4427.8	90.8
1981	3719.6	3995.8	93.1
1982	3874.9	4103.3	94.4
1983	3704.9	3706.9	100.0
1984	3642.4	3646.4	99.9
1985	3331.3	3254.0	102.4
1986	3088.1	2987.9	103.4
1987	3109.6	3016.8	103.1
1988	3102.8	3035.0	102.2
1989	3416.6	3346.1	102.1
1990	3206.3	3203.0	100.1
1991	3415.3	3337.3	102.3
1992	3336.0	3005.4	111.0

TABLE 7

THREE-YEAR MOVING AVERAGE FOR GRAIN YIELD OF THE ADVANCED WHEAT PERFORMANCE NURSERY (AWPN) AND STANDARD CULTIVAR IN THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Harvest	Three-Year Moving Average for Grain Yield		
Year	AWPN	Standard	AWPN
	--------- kg ha^{-1} ---------		% of Standard
1970	3083.4	3245.3	95.0
1971	2810.6	3068.6	91.6
1972	2829.4	3216.4	88.0
1973	2698.4	2951.7	91.4
1974	2940.2	3095.4	95.0
1975	2963.1	2900.6	102.2
1976	3147.9	3205.0	98.2
1977	3182.8	3240.6	98.2
1978	3689.4	3883.6	95.0
1979	3764.7	3962.2	95.0
1980	4149.7	4392.2	94.5
1981	4007.2	4120.8	97.2
1982	4147.0	4058.3	102.2
1983	3752.6	3538.9	106.0
1984	3657.8	3451.6	106.0
1985	3396.5	3193.5	106.4
1986	3218.4	3095.4	104.0
1987	3149.2	3005.4	104.8
1988	3067.9	3146.5	97.5
1989	3329.3	3307.8	100.7
1990	3135.8	3155.9	99.4
1991	3360.2	3157.9	106.4
1992	3336.0	3005.4	111.0

TABLE 8

THREE-YEAR MOVING AVERAGE FOR TEST WEIGHT OF THE INTERMEDIATE WHEAT PERFORMANCE NURSERY (IWPN) AND STANDARD CULTIVAR IN THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Harvest Year	Three-Year Moving Average for Test Weight		
	IWPN	Standard	IWPN
	---------- $kg\ m^{-3}$ -------		% of Standard
1970	787.6	777.1	101.4
1971	787.0	779.4	101.0
1972	782.0	778.9	100.4
1973	774.4	780.1	99.3
1974	762.7	765.9	99.6
1975	769.0	770.4	99.8
1976	767.6	762.3	100.7
1977	770.3	769.0	100.2
1978	769.0	769.6	99.9
1979	768.1	773.9	99.3
1980	766.8	772.2	99.3
1981	757.5	765.1	99.0
1982	760.5	762.8	99.7
1983	759.3	765.1	99.2
1984	754.2	759.3	99.3
1985	745.0	753.2	98.9
1986	724.6	735.3	98.6
1987	734.4	745.6	98.5
1988	734.5	745.2	98.6
1989	752.3	755.9	99.5
1990	744.7	746.1	99.8
1991	747.1	745.2	100.3
1992	735.9	735.0	100.1

TABLE 9

THREE-YEAR MOVING AVERAGE FOR TEST WEIGHT OF THE ADVANCED WHEAT PERFORMANCE NURSERY (AWPN) AND STANDARD CULTIVAR IN THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Harvest Year	Three-Year Moving Average for Test Weight AWPN	Standard	AWPN
	--------- $kg\ m^{-3}$ ---------		% of Standard
1970	771.9	762.9	101.2
1971	778.0	770.4	101.0
1972	787.1	779.4	101.0
1973	775.9	772.6	100.4
1974	763.2	763.3	100.0
1975	765.5	766.5	99.9
1976	770.3	770.8	99.9
1977	775.7	774.4	100.2
1978	771.8	773.9	99.7
1979	757.8	764.1	99.2
1980	760.9	767.1	99.2
1981	752.9	757.1	99.4
1982	765.9	763.2	100.4
1983	758.4	755.5	100.4
1984	750.6	754.2	99.5
1985	743.2	751.2	98.9
1986	723.4	737.8	98.1
1987	735.8	746.1	98.6
1988	734.5	743.0	98.9
1989	756.2	756.8	99.9
1990	740.0	743.5	99.5
1991	742.2	741.7	100.1
1992	727.3	725.6	100.2

TABLE 10

THREE-YEAR MOVING AVERAGE FOR HEADING DATE OF THE INTERMEDIATE WHEAT PERFORMANCE NURSERY (IWPN) AND STANDARD CULTIVAR IN THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Harvest Year	Three-Year Moving Average for Heading Date IWPN	Standard	IWPN
	no of days after March 31		% of Standard
1970	33.6	33.7	99.8
1971	30.4	30.6	99.2
1972	31.8	31.9	99.8
1973	32.0	34.1	93.9
1974	36.9	38.3	96.1
1975	32.8	33.2	98.7
1976	28.9	26.8	107.5
1977	28.3	27.0	104.9
1978	32.1	32.3	99.2
1979	39.8	40.7	97.9
1980	38.8	38.3	101.1
1981	38.1	37.3	102.1
1982	38.6	38.8	99.3
1983	43.1	43.3	99.4
1984	42.2	41.0	103.0
1985	34.6	31.5	109.8
1986	30.9	27.7	111.6
1987	32.6	31.0	105.1
1988	35.7	34.3	104.1
1989	36.5	35.0	104.3
1990	32.7	30.7	106.8
1991	33.1	31.0	106.7
1992	30.2	29.0	103.9

TABLE 11

THREE-YEAR MOVING AVERAGE FOR HEADING DATE OF THE ADVANCED WHEAT PERFORMANCE NURSERY (AWPN) AND STANDARD CULTIVAR IN THE OAES WHEAT BREEDING PROGRAM, 1969 TO 1993.

Harvest Year	Three-Year Moving Average for Heading Date		
	AWPN	Standard	AWPN
	no of days after March 31		% of Standard
1970	32.0	33.7	95.0
1971	29.1	30.3	95.9
1972	32.1	32.3	99.6
1973	33.2	32.8	101.4
1974	38.4	37.2	103.3
1975	33.7	33.2	101.5
1976	32.7	32.5	100.7
1977	33.5	34.2	97.9
1978	38.8	37.3	104.0
1979	41.7	41.7	100.0
1980	36.6	36.2	101.2
1981	34.9	34.5	101.1
1982	35.5	35.8	99.1
1983	42.8	44.0	97.3
1984	42.8	42.7	100.3
1985	35.5	33.7	105.5
1986	31.4	27.7	113.3
1987	33.5	30.7	109.2
1988	35.8	34.0	105.2
1989	36.1	35.0	103.0
1990	32.0	31.0	103.2
1991	28.5	27.7	103.0
1992	29.9	29.0	103.2

VITA

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