ALTERNATIVE SELECTION STRATEGIES FOR

WINTER WHEAT IMPROVEMENT

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Submitted to the Faculty of the
Graduate College of the
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in partial fulfillment of
the requirements for
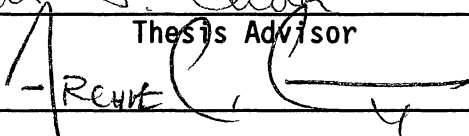the Degree of
DOCTOR OF PHILOSOPHY
December, 1991

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Thesis Approved:

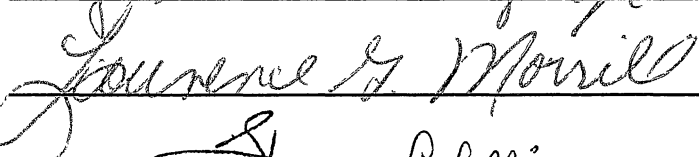_____
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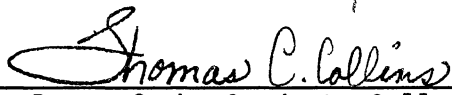
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ACKNOWLEDGEMENTS

The author wishes to extend his appreciation to Dr. Brett F. Carver, major advisor, for his guidance throughout the course of this study. Sincere appreciation is also extended to the other members of my committee, Dr. Archie C. Clutter, Dr. Lawrence G. Morrill, and Dr. Eugene G. Krenzer, Jr., for their advice offered in the preparation of this thesis.

The author is grateful to the Agronomy Department of Oklahoma State University for the facilities made available for this study. Priscilla K. Milan is deserving of special thanks for providing computer facilities for typing and preparing this thesis.

My deep respect and gratitude is sincerely expressed to the government of Pakistan for financial assistance and concern.

Special appreciation is expressed to my wife, Tahira, and my little sons, Waqas M. Nasir and Ilyas M. Nasir, for their patience and sacrifice during the preparation of this thesis.

Finally, to the memory of my beloved mother and father, I dedicate this thesis.

TABLE OF CONTENTS

LIST OF TABLES

Chapter II

Chapter III

CHAPTER I

INTRODUCTION

Chapters II and III of this thesis are separate and complete manuscripts to be submitted to _Euphytica_ and _Crop Science_, respectively.

CHAPTER II

Simultaneous Genetic Improvement of Wheat Yield in Drought-stressed and Irrigated Environments

Summary

Wheat (<u>Triticum</u> <u>aestivum</u> L.) cultivars grown in the southern Great Plains of the USA are exposed to a wide range of moisture conditions due to large fluctuations in the amount and frequency of rainfall. The objectives of this investigation were to 1) examine various genetic parameters for grain production in drought-stressed and irrigated environments and evaluate relationships among those parameters, 2) determine a selection criterion which maximizes yield responses in both drought-stressed and irrigated environments.

Seventy F_2-derived wheat lines from the cross, TAM W-101/Sturdy, were evaluated at Goodwell, OK under irrigated and natural drought-stressed conditions in 1987 and 1988.

Genetic variance and heritability estimates were higher in the irrigated environment than those in the drought-stressed environment. Genetic correlation between yields in the two environments was 0.20 ± 0.16 indicating that identification of widely adapted genotypes requires tests in both environments. The selection index, $I = .7Y_1 + .3Y_2$, where Y_1 and Y_2 are yields in irrigated and drought-stressed environments, respectively, was equally efficient or superior to other indices based on genetic gain in each environment and was most efficient for genetic gain across both environments. The results indicate that an index comparable to mean productivity should identify genotypes with superior yield potential in both drought-stressed and irrigated environments.

Introduction

Wheat production in the southern Great Plains of the USA is often
limited by sub-optimal moisture conditions. Large fluctuations occur in
the amount and frequency of rainfall events from year to year and among
locations within years. Hence, wheat producers in this region need
cultivars that produce high yields under good growing conditions while
suffering minimum loss during droughty seasons. Wheat breeders are thus
challenged by the difficult task of developing cultivars with wide
adaptation, even within a geographically narrow region. Keim & Kronstad
(1979) proposed that an ideal cultivar for stress-prone environments
should have high yield in the most severely stressed environment
expected yet have a strong response to increasing productivity levels.

One issue extensively scrutinized is whether breeding for stress
environments should rely on tandem selection in optimal and stress
environments, or on direct selection in stress environments only
(Ceccarelli, 1989). Several researchers have concluded that selection
under favorable conditions produces genotypes that are suitable for both
stress and nonstress environments (Frey, 1964; Roy & Murty, 1970; Laing
& Fischer, 1979; Quisenberry, et al., 1980; Johnson & Geadelmann, 1989).
Whitehead & Allen (1990) tested the hypothesis that some soybean
genotypes have superior yield potential in both low- and high-stress
edaphic conditions and, therefore, evaluation in low-stress environments
can be used effectively to select such genotypes. On the other hand,
several other authors have concluded that yield improvement under high-
stress conditions requires selection strictly under those conditions
(Arboleda-Rivera & Compton, 1974; Ceccarelli, 1987; Ceccarelli, 1989;
Atlin, 1989). Whether direct or indirect selection is superior depends

upon the heritabilities of the selected trait in stress and nonstress
environments and the genetic correlation between stress and nonstress
environments (Atlin & Frey, 1989). Ceccarelli (1989) noted that it is
not the relative magnitude of heritability in nonstress vs. stress
environments which determines the optimal environment for selection, but
the extent to which differences between genotypes observed under a given
environment are maintained in a different environment. Thus, the
magnitude of genetic correlation between the two environments is more
important than the relative magnitude of heritability in determining the
selection environment.

This issue was theoretically examined by Rosielle & Hamblin (1981)
who defined stress tolerance as the difference in yield between stress
and nonstress environments (i.e., the yield loss resulting from stress)
and mean productivity as mean yield of a genotype across the two
environments. They showed that selection for tolerance would improve
yield in the stress environment, albeit at the expense of reducing yield
in the nonstress environment and therefore mean productivity. Only in
the rare situation where genetic variance in the stress environment
exceeds that in the nonstress environment and the genetic correlation
between environments is high would mean productivity and tolerance be
positively correlated. Therefore, selection for tolerance would be
worthwhile only when yield improvement in stress environments is
imperative. Tolerance and mean productivity are only two of an infinite
number of linear combinations of yield measured in the two environments
(treated as two distinct traits). Mean productivity is simply an
arithmetic average of two traits (equal weighting of the two yield
measurements), while tolerance is their differential (weights of +1

and -1). Further study is needed to determine if other linear combinations, or indices, better utilize the particular variance/covariance parameters of a given population.

Bruckner and Frohberg (1987) also combined information from stress and nonstress environments into a "stress susceptibility" index, defined for a genotype as $S = (1-Y_D/Y_P)/D$, where Y_D is yield in the stress environment, Y_P is yield in the nonstress environment (potential yield) and $D = 1 - $ (mean Y_D of all genotypes/mean Y_P of all genotypes). Spring wheat genotypes with low S values for grain yield did not show outstanding yield performance in stress environments due to low yield potential, but did suffer minimum yield loss (high tolerance) from stress.

Avoiding low yields is important to producers at any production level (Eskridge, 1990). Therefore, the objectives of this investigation were to 1) examine various genetic parameters for grain production in drought-stressed and irrigated environments and evaluate relationships among those parameters, and 2) determine an optimum selection criterion for simultaneous genetic improvement of grain yield in drought-stressed and irrigated environments in an experimental bread wheat population.

Materials and methods

Experimental materials used in this study consisted of 70 F_2-derived F_4 [$F_{(2)4}$] lines in 1986-1987 and 70 $F_{(2)5}$ lines in 1987-1988 having the pedigree, TAM W-101/Sturdy. Lines were assigned to two maturity groups (early and late) based on heading dates of F_3 parents. TAM W-101 is considered drought resistant and Sturdy is considered drought susceptible (Tahara et al., 1990); therefore, this population was expected to provide a wide array of phenotypes for reaction to drought stress. Experiments were conducted at Goodwell, OK on a Richfield clay loam soil (fine, mixed, montmorillonitic, mesic Aridic Argiustolls), under irrigated and dryland (rainfed) conditions. Because Goodwell is reputed for drought stress and because furrow irrigation was available in neighboring fields, it was a suitable location to impose drought stressed and well-watered conditions under otherwise equal environmental conditions. Respective average grain yields from 1986 to 1990 in breeders' trials were 2066 and 4148 kg ha^{-1} (E.L. Smith, personal communication).

The experimental design was a nested split-plot in each environment (drought-stressed and irrigated). The two maturity groups were assigned to main plots while the 35 lines per group, plus one parent, were assigned to subplots. TAM W-101 was included in the late maturity group while Sturdy was included in the early maturity group. There were three replications in each environment.

Data were collected on heading date and grain yield. Univariate and multivariate analyses of variance were conducted within single environments and across environments, respectively, to determine genetic

parameters and overall performance of genotypes. The following definitions were used according to Rosielle and Hamblin (1981);

$$\text{Yield in the irrigated environment} = Y_1$$

$$\text{Yield in the stress environment} = Y_2$$

$$\text{Tolerance to stress} = Y_3 = Y_2 - Y_1$$

$$\text{Mean productivity} = Y_4 = (Y_1 + Y_2)/2$$

Genetic variances were computed in each environment across years from the lines-within-maturity group source of variance. Genetic variances were denoted as G_{11} (irrigated environment) and G_{22} (drought-stressed environment). Magnitudes of G_{11} and G_{22} were compared on an absolute basis and tested for heterogeneity via an F-test of the larger variance divided by the smaller variance. Genetic variances were also compared on a relative basis (genotypic CV). The ratio of genetic variances in stress and nonstress environments was computed as $K^2_G = G_{22}/G_{11}$. Heritability estimates for grain yield in each of the irrigated and dry environments were computed on entry-mean basis from the components of analysis of variance combined over years to reduce GE bias. Standard errors for heritabilities were calculated according to formula of Hanson (1989).

The genetic correlation between grain yields in stress and irrigated environments (r_{G12}) was computed from the lines-within-maturity group sources of variance and covariance between years, i.e., between Y_1 in 1987 and Y_2 in 1988, and vice versa. The between-year analysis of covariance was used to reduce genotype-environment interaction bias and thereby provide an approximation of r_{G12}. A standard error for the genetic correlation was calculated according to

Falconer (1989). Values of K^2_G and r_{G12} were used to determine expected relationships between:

a) stress tolerance and yield in irrigated environments (r_{G13}),

b) stress tolerance and yield in drought-stressed environments (r_{G23}),

c) mean productivity and yield in irrigated environments (r_{G14}),

d) mean productivity and yield in drought-stressed environments (r_{G24}), and

e) stress tolerance and mean productivity (r_{G34}),

using formulae developed by Rosielle and Hamblin (1981).

Seven selection indices (Table 1) were constructed to determine simultaneous genetic advance for yields in irrigated and drought-stressed environments. These indices were designed to place varying proportions (0-100%) of weight on yields in irrigated and drought-stressed environments (I-1 to I-5), as well as consider two alternative indices referred to as stress tolerance (I-6) and a modified susceptibility index (I-7), where the constant D was removed from the expression. The best six lines (three from each maturity group) were selected according to their index score. All analyses were performed within maturity groups to remove potential bias of maturity differences on yield performance. Progeny evaluation (all lines) in 1987-1988 was used to assess response to selection on the index. Selection responses were computed by subtracting the population mean yield from mean yield of the selected lines in each maturity group in each environment. Responses from the two environments were added to compute total response for each index. Selection efficiency was compared in individual environments and across both environments.

Results and discussion

Rainfall during the 1986-87 and 1987-88 crop seasons was slightly higher than the long-term average at Goodwell (Table 2) but was still within the range of typical dryland environments (Duley & Coyle, 1955). Grain yield in the irrigated environment averaged 3484 kg ha^{-1}, whereas grain yield under dryland conditions averaged 1663 kg ha^{-1}, more than a 50% reduction. Mean grain yields of Sturdy and TAM W-101 (1988 only) were 4219 and 4609 kg ha^{-1} under irrigated conditions and 2024 and 2274 kg ha^{-1} under dryland conditions. Classification of lines into groups differing by heading date was somewhat successful. Averaged across years, the early group headed about 2 days earlier than later group under dryland or irrigated conditions (Table 3); however, significant variation was still detected among lines within groups for heading date (Table 4). Drought tolerance of these lines will be assessed within groups to reduce the confounding bias of drought escape.

Under irrigated conditions, there was no significant difference in grain yield between groups (Tables 3 and 4). Under dryland conditions, the early group had significantly ($P < .01$) higher grain yield than the late group when compared in each year (data not shown), but no significant difference was found when averaged across years due to significant year x group interaction (Table 4). Higher grain yield of the early group in the dryland environment is consistent with earliness providing a drought-escape mechanism (Blum, 1985).

Significant variation was detected for grain yield among lines within groups in each environment (Table 4), indicating the population segregated for genes conditioning yield potential and drought tolerance.

Genetic variance for grain yield in the irrigated environment was about 3.5 times greater than in the dryland environment (Table 5). Genetic variances were heterogeneous when compared on an absolute basis but were similar in magnitude relative to the mean. Genotypic C.V.'s were 6.4% (irrigated) and 7.2% (dryland). Error variances were about six- and two-times higher than the respective genetic variances in dryland and irrigated environments. Blum (1985) also noted that stress causes a reduction in the genetic variance and heritability for yield, which consequently limits selection efficiency for yield under stress. Allen et al. (1978) indicated that the relative magnitude of genotypic variance in different environments is crop-specific. In soybean, and especially in wheat, the genotypic variance in favorable environments was several times greater than in unfavorable environments. Johnson & Frey (1967) also found that both genotypic variance and environmental variance increased as the value, measured by grain yield, of the environment increased.

The genetic correlation between grain yields in dryland and irrigated environments was only 0.20 and did not differ significantly from zero (Table 5). The correlation indicates that any gain from selection in this population in irrigated environments will not be expressed under dryland conditions, and vice versa. The assumption that lines with high yield potential under optimal conditions also express their superiority under drought-stressed conditions could not be confirmed in this population. None of the top three yielding lines in each group was common to both environments. Therefore, within the normal range of selection intensity, no line possessed the best combination of favorable genes for high yield potential in both high-

productivity and low-productivity environments. These results agree with findings of many researchers (Ceccarelli, 1987; Ceccarelli, 1989; Atlin & Frey 1989; Ehdaie et al., 1988), but at the same time they contrast with others (Frey, 1964; Roy & Murty, 1970; Quisenberry, et al., 1980; Johnson & Geadelman, 1989; Whitehouse & Allen, 1990). Identification of widely adapted lines seemingly require tests in both stress and nonstress environments.

The heritability estimate for grain yield in the irrigated environment was slightly higher than that in the dryland environment (Table 5); but indistinguishable based on their standard error. High heritabilities for grain yields in nonstress environments have been previously reported (Frey, 1964; Roy & Murty, 1970). Depending on the relative magnitudes of genetic and error variance, heritability for oat grain yield was sometimes greater and sometimes less in the better environments (Johnson & Frey, 1967). Ceccarelli (1989) reported no clear trend of heritabilities for grain yield in barley bulks when grown in two contrasting environments. High heritability in nonstress environments has been used (Ceccarelli, 1989) as an argument for selecting only under nonstress conditions even if the target is stress environment. Heritabilities in this study do not suggest that selection must be conducted under optimum conditions for improving drought tolerance in the dryland environment. Responses in Table 6 indeed indicate that selection under irrigated conditions was less effective for improving grain yield under drought stress environment than direct selection under stress environment. Ceccarelli et al. (1987) reported that genetic differences for wheat grain yield in the absence of stress were largely unrelated with differences in the presence of severe

stress. Data obtained with maize (Loffler et al., 1986) lead to the same conclusion. Atlin & Frey (1989) demonstrated that grain yield in stress or low-productivity environments and grain yield in high-productivity environments were not controlled by the same genes.

Drought tolerance can be defined as the yield reduction incurred by a genotype under drought stress; thus selection for tolerance would favor lower negative values of Y_2-Y_1. Based on our values of K^2_G and r_{G12}, and formulae provided by Rosielle and Hamblin (1981), the expected genetic correlation between stress tolerance (Y_3) and irrigated yield (Y_1) i.e., r_{G13} was -0.86 (Table 5). Thus, selection for tolerance will decrease yield in the irrigated environment and thus decrease average yield in both environments. The expected genetic correlation between stress tolerance and yield in the dryland environment (r_{G23}) was 0.33, indicating that selection for stress tolerance should give a positive response under stress. Therefore, selection for tolerance will be worthwhile only when the target is a stress environment. The expected genetic correlations between mean productivity and yields in the irrigated (r_{G14}) and dryland environments (r_{G24}) were 0.90 and 0.66, respectively. Thus selection for mean productivity should give positive responses in both environments. The expected genetic correlation between stress tolerance and mean productivity was negative (r_{G34} = -0.59, Table 5) indicating that selection for tolerance will produce lines with low yield potential under irrigated conditions or selection for mean productivity will produce lines with less tolerance to drought.

While these results indicate the direction of selection response, they do not provide quantitative estimates needed for more detailed

comparisons of these and other indices. Using the tests in 1988 to measure response to selection in the previous year, we tested the hypothesis that some other linear, or possibly a nonlinear combination, of Y_1 and Y_2 result in greater response to selection. Gains from index-2 ($.3Y_1 + .7Y_2$), index-3 or mean productivity ($.5Y_1 + .5Y_2$) and index-6 or tolerance ($Y_2 - Y_1$) were similar under dryland conditions, averaging 356 kg ha^{-1} (Table 7). Response for index-7 (Y_2 /Y_1) was 191 kg ha^{-1} while index-5 (Y_1 only) gave only a modest response in dryland environment. Selection response for index-1 (Y_2 only) was intermediate (312 kg ha^{-1}). Index-4 ($.7Y_1 + .3Y_2$) gave the maximum response in the dryland environment (391 kg ha^{-1}). To maximize selection response in the dryland environment, some information (70%) on yield from the irrigated environment is apparently beneficial. Responses of all indices were positive in the dryland environment.

Under irrigated conditions, responses of the various indices were mixed in sign (Table 8). Index-5 (Y_1 only) gave the maximum response (768 kg ha^{-1}) but was only slightly better than index-4 ($.7Y_1 + .3Y_2$). Mean productivity ($.5Y_1 + .5Y_2$) also gave a positive but much smaller response (244 kg ha^{-1}). Index-1 (Y_2 only), index-6 ($Y_2 - Y_1$), and index-7 (Y_2 /Y_1) gave negative responses in the irrigated environment.

Because our ultimate breeding objective is to select lines for wide adaptation, we also compared selection response pooled across both environments. As expected from above, index-4 ($.7Y_1 + .3Y_2$) gave the maximum response of 1070 kg ha^{-1} (34% of the population mean) for grain yield (Table 9). Responses for other indices ranged from 148 (index-7) to 864 (index-5) kg ha^{-1} (8 - 23% of population mean). Therefore,

index-4 was the only index which provided substantive responses in both environments and therefore resulted in maximum total response.

By employing Index-4 in this population, yields in both the stress and nonstress environments should increase and to a greater extent than mean productivity. Neither the irrigated or dryland environment alone was optimum for increasing yield under drought stress. In order to achieve maximum response in the stress environment information is needed from both environments. The most desirable approach would be that testing sites should also include stress environments so that stress tolerant genotypes are not lost in early segregating generations due to selection practiced only in favorable environments.

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Table 1. Selection indices and their relative weights for grain yield in irrigated and dryland environments at Goodwell, OK

Selection index	Relative Weight Y_1	Y_2
1	0.0	1.0
2	0.3	0.7
3	0.5	0.5
4	0.7	0.3
5	1.0	0.0
6	-1.0	1.0
7	-	$1/Y_1$

Table 2. Long-term average monthly rainfall and rainfall in 1986-1987 and 1987-1988 growing seasons at Goodwell, OK

Month	Long-term	1986-1987	1987-1988
		mm	
September	31.75	9.75	88.75
October	23.75	17.25	2.50
November	16.00	53.50	13.50
December	6.75	12.25	9.25
January	6.25	11.75	8.25
February	7.75	29.25	0.50
March	19.50	31.06	19.50
April	27.75	0.00	63.25
May	71.75	156.50	62.25
Total	211.25	321.31	267.75

Table 3. Means for days to heading (days after April 30) and grain yield of lines in early and late groups within environments and years

Environment	Group	1987 Days to heading	1987 Grain yield	1988 Days to heading	1988 Grain yield
		no.	kg ha^{-1}	no.	kg ha^{-1}
Irrigated	Early	3.4	2818	11.5	4158
	Late	5.4	2874	12.9	4086
	Mean		2846		4122
Dryland	Early	8.0	1159	12.5	2268
	Late	9.5	1019	14.6	2208
	Mean		1089		2238

Table 4. Selected mean squares for days to heading, (days after April 30) and grain yield (kg ha^{-1}) of 70 wheat lines at Goodwell, OK, under irrigated and dryland conditions across two years

Source	df	Irrigated		Dryland	
		Days to heading	Yield (X 10^3)	Days to heading	Yield (X 10^3)
Year[a]	1	6,529	171,062	2,371	138,651
Group[b]	1	322**	8	340	1,046
Year X Group	1	14	421	10	160**
Line/Group	68	6**	495**	4**	199**
Early group	34	5**	617**	3**	193**
Late group	34	7**	373**	6**	205**
Year X Line/Group	68	2**	198**	2**	113
Pooled error	272	0.9	109	0.8	92

[a] Not tested for significance due to lack of true error term.

[b] The 70 lines were divided into two groups of 35 lines each based on heading dates (early and late) of F$_3$ parents.

Table 5. Genetic and error variances for grain yield under irrigated and dryland conditions, their ratio, heritabilities of and genetic correlation between yields in irrigated and dryland environments and genetic correlations among stress tolerance, mean productivity and their components

Statistic[a]	Value
G_{11}	49439 ± 15022
G_{22}	14344 ± 6447
V_E (Irrigated)	109448± 9351
V_E (Dryland)	92056 ± 7865
K^2_G	0.29
h^2 (Irrigated)	0.60 ± 0.10
h^2 (Dryland)	0.43 ± 0.14
r_{G12}	0.20 ± 0.16
r_{G13}	-0.86
r_{G23}	0.33
r_{G14}	0.90
r_{G24}	0.66
r_{G34}	-0.59

[a] 1 = Irrigated environment value   2 = Dryland environment value

3 = Stress tolerance   4 = Mean productivity

Table 6. Mean yield (kg/ha) of selected lines ($\bar{x}_s$) and of the whole population ($\bar{x}_0$), the selection differential (S), and the response to selection (R) of lines selected in either irrigated or drought-stressed environments

Selection environment	Test environment	
	Irrigated	Dryland
Irrigated	$\bar{x}_s$ early group = 4598	$\bar{x}_s$ early group = 2329
	$\bar{x}_s$ late group = 4414	$\bar{x}_s$ late group = 2243
	$\bar{x}_0$ early group = 4158	$\bar{x}_0$ early group = 2268
	$\bar{x}_0$ late group = 4086	$\bar{x}_0$ late group = 2208
	S early group = 440	S early group = 61
	S late group = 328	S late group = 35
	S total = 768	S total = 96
	R = 461	R = 41
Dryland	$\bar{x}_s$ early group = 4323	$\bar{x}_s$ early group = 2356
	$\bar{x}_s$ late group = 3880	$\bar{x}_s$ late group = 2433
	$\bar{x}_0$ early group = 4158	$\bar{x}_0$ early group = 2268
	$\bar{x}_0$ late group = 4086	$\bar{x}_0$ late group = 2208
	S early group = 165	S early group = 88
	S late group = -206	S late group = 225
	S total = -41	S total = 313
	R = -18	R = 134

Table 7. Selection responses for grain yield under dryland conditions at Goodwell, OK in 1987-1988

Selection index	Weight		Group		
	Y_1	Y_2	Early	Late	Combined
				kg ha^{-1}	
1	0.0	1.0	87	225	312
2	0.3	0.7	38	320	358
3	0.5	0.5	38	315	353
4	0.7	0.3	76	315	391
5	1.0	0.0	60	36	96
6	-1.0	1.0	136	222	358
7	-	$1/Y_1$	136	55	191

Table 8. Selection responses for grain yield under irrigated conditions at Goodwell, OK in 1987-1988

Selection index	Weight Y_1	Y_2	Group Early	Late	Combined
				kg ha^{-1}	
1	0.0	1.0	65	-206	-141
2	0.3	0.7	74	-42	32
3	0.5	0.5	74	170	244
4	0.7	0.3	509	170	679
5	1.0	0.0	440	328	768
6	-1.0	1.0	-21	-110	-131
7	-	$1/Y_1$	-21	-22	-43

Table 9. Total selection responses for grain yield across environments at Goodwell, OK in 1987-88

Selection index	Weight Y_1	Y_2	Grain yield
			kg ha^{-1}
1	0.0	1.0	171
2	0.3	0.7	390
3	0.5	0.5	597
4	0.7	0.3	1,070
5	1.0	0.0	864
6	-1.0	1.0	227
7	-	$1/Y_1$	148

CHAPTER III

Visual Selection for Forage Yield

in Winter Wheat

ABSTRACT

Winter wheat (<u>Triticum</u> <u>aestivum</u> L.) is used as both a grain and forage crop in the southern Great Plains, but wheat improvement programs traditionally focus on grain characteristics when determining the genetic worth of experimental strains. Conventional clipping tests of large populations are cost-prohibitive and often unfeasible due to limited seed supply in early generations. Therefore, accurate prediction of forage yields from visual estimates of small plots would appeal to breeders. The objectives of this study were to measure the response to divergent visual selection for forage yield based on a season-long visual index and to quantify relationships among forage yield and grain yield of clipped and conventional plots. Six high and 6 low forage-producing lines were selected from each of three F_4 populations based on an index comprised of forage characteristics and growth habit during vegetative growth. The 36 selections and their parents were tested in the F_5 (1988-1989) and F_6 (1989-1990) generations. The high-selection group generally exceeded the low-selection group in fall forage yield measured prior to winter dormancy, but that response did not prevail for winter forage yield measured after dormancy but before jointing. There was no significant relationship between forage yield and grain yield of clipped or conventional plots, but the correlation between grain yield under clipped and non-clipped

28

conditions was positive (r=0.39, P<0.01, df=43). In conclusion, visual selection was effective in manipulating fall forage yield. Success in improving forage yield, however, does not guarantee the same for grain yield.

INTRODUCTION

Winter wheat is used as both a grain and forage crop in the southern Great Plains. The economic return from wheat includes the combined value of grain and beef produced. Generally, the wheat crop is grazed during vegetative growth in the fall and winter, before removing the cattle in early spring to produce a grain crop (Thompson, 1990).

Despite the apparent need to apply direct selection for forage characteristics during cultivar development, evaluation of forage potential usually comes after cultivar release (Worrall and Gilmore, 1985; Krenzer et al., 1988; West et al., 1988). Conventional clipping tests of large populations are prohibitive in cost and time, if not unfeasible due to limited seed supply in early generations. Selection pressure could be imposed if strains were evaluated visually in relatively small plots.

Published literature on visual selection for forage yield in winter wheat and other small grains is limited. However, differences exist regarding the success of visual selection for grain yield (Boyce et al, 1947; Lupton and Whitehouse, 1955; Mckenzie and Lambart, 1961; Krull et al, 1966). Atkins et al. (1969) did find significant correlation (r=0.55 to 0.66) between visual estimates of forage yield and clipped forage yields of oat and barley strains. They concluded that visual estimates can be applied with confidence in a forage selection program. Subsequent to their study, very few breeding programs have considered forage characters during inbred line

30

development to the same extent as grain characters. Forage characters amenable to visual selection are tillering capacity, leaf size, canopy height, growth habit (prostrate to upright) and regrowth potential after forage removal.

Visual selection is the oldest form of plant breeding practiced by man. Its effectiveness on highly heritable characters in self-pollinated species is widely accepted, but for lowly heritable traits such as yield, its effectiveness is debatable. The objectives of this study were to determine the success of divergent visual selection for forage yield based on a season-long visual index and to quantify relationships among forage yield and grain yield of clipped and conventional plots.

MATERIALS AND METHODS

During the 1987-1988 growing season, three F_4 populations of 80 lines each were evaluated in randomized complete blocks with two replications near Stillwater, OK (Norge loam, fine-silty, mixed, thermic Udic Paleustolls). Their pedigrees were 'Chisholm'//OK79257/OK82377 (Population 1), '2165'/'Arkan' (Population 2), and Arkan/OK79256 (Population 3). Parents were chosen on the basis of differences in forage and grain yields. Each line was planted in the two center rows of a four-row plot (0.3 x 3 m). Seed of the corresponding parents were blended in equal amounts and planted in the two border rows. Plots were visually rated for forage yield using a scale of -2 to +2 to represent undesirable (negative values) to desirable (positive values) forage characteristics. Ratings were based on leaf size, tillering capacity, canopy height, and general vigor relative to the parent blend in neighboring border rows of each plot. A value of zero implied no visual difference between the experimental line and parent blend.

Three visual ratings were recorded during the growing season (Oct. 10, 1987; Feb. 2, 1988; and March 7, 1988) for long-term (LT) forage yield. On each date, the entire plot area was cut with a rotary mower to an approximate height of 5 cm. Seven to ten days later, plots were rated for short-term (ST) regrowth using the same scale as before. Growth habit was also monitored where forage ratings were made. Prostrate types were assigned a score of -1 for their perceived undesir-

able forage production potential. Semi-erect and erect types were assigned a neutral score of 0. A total forage index was constructed by summing three LT and two ST forage ratings and five growth habit scores. Two selection groups were formed in each population by selecting six lines with the highest index values (high-forage, HF, selection group) and six with the lowest values (low-forage, LF, selection group).

The 36 selections were tested the following year (1988-1989) in replicated forage and grain yield trials at Perkins (Teller loam , fine-loamy, mixed, thermic Udic Argiustolls) and Stillwater, OK. Also tested were their parents and three checks, including 'TAM 200', 'Thunderbird', and a 50:50 blend of TAM 200 and Thunderbird. All plots were 0.3 m x 3.0 m and planted entirely with each entry, except for one experiment planted at Stillwater as described later. Genotypes were arranged in a randomized complete block design for each trial. Plots were planted with seed harvested from plots visually selected in 1987-1988.

The forage trial at Perkins was planted on Aug. 30, 1988 with four replications. Forage yields were obtained during the fall (prior to dormancy) and late winter (after dormancy) by clipping a 1.2 m section of one interior row ca. 5 cm above-ground. Harvest dates were Oct. 24, 1988, Jan. 5, 1989, and March 15, 1989. Each measurement was separated by 4 wk or more and therefore designated as LT estimates of forage yield. All remaining forage was removed by a rotary mower to a uniform canopy height (ca. 5 cm) immediately after each harvest. Short-term (ST) forage regrowth, when measurable, was clipped 7 to 10 d later from a 1.2 m section of a different interior row than that used to determine LT forage yield. Forage samples were oven-dried at 49°C for 72 hr before weighing. Total fall forage yield was obtained by adding the LT

and ST estimates in 1988. Total winter forage was computed by adding
the two LT estimates in January and March (hereafter referred to as LT-1
and LT-2) and one ST estimate in March. Total forage yield in 1988-1989
was obtained by combining total fall and total winter forage yields.

Two trials were conducted at Stillwater. One was planted early
(Aug. 31, 1988) and conducted similar to the selection experiment in
1987-1988 but with three replications. Visual ratings were made
throughout the vegetative stage for forage yield, regrowth, and growth
habit at the same time forage yield was determined in the Perkins trial.
Plots were also harvested for grain yield to determine yield potential
under pseudo-grazing conditions. The second trial in Stillwater was
planted conventionally (Oct. 13, 1988) with four replications and was
harvested for grain yield only. The two experiments were placed
adjacent to each other in the same field so that yield comparisons could
be made with minimum environmental bias.

All experiments were repeated in 1989-1990 at the same sites to
gain another measurement of selection response. The forage yield trial
at Perkins was planted on Aug. 30, 1989; planting dates for the two
experiments at Stillwater were Sept. 8, 1989 and Oct. 15, 1989. Forage
harvest dates at Perkins were Oct. 24, 1989 (fall LT-1), Nov. 3, 1989
(fall ST), Nov. 21, 1989 (fall LT-2), Feb. 6, 1990 (winter LT-1), March
4, 1990 (winter LT-2), and March 15, 1990 (winter ST). Total fall
forage was computed by summing fall LT-1 and LT-2, while total winter
forage was computed by summing winter LT-1, LT-2, and ST. Total forage
yield in 1989-1990 was found by adding total fall and total winter
forage yields. Harvest procedures and visual ratings at Stillwater were
conducted as in the previous year.

Forage data were analyzed separately for each year due to different sampling schedules between the two years. Grain yield was analyzed by combining data from both years. Statistical analyses centered upon comparison of the HF selection group vs. the LF selection group, i.e., the magnitude of the selection response. The hypothesis for testing was that the HF selection groups produced higher visual index values and therefore higher forage yields than the LF selection groups. The association between forage and grain production was also examined to determine the potential for preserving high grain yield potential when selecting for high forage yield.

RESULTS AND DISCUSSION

The 1988-1989 wheat growing season was one of extremes (Krenzer et al., 1989). Sufficient rainfall in mid-September was followed by unusually low rainfall in October and November, 1988. Hence forage production was limited by lack of water. Temperatures were extremely moderate in December 1988, January and early February 1989, only to be followed by an abrupt freeze in late February. The 1989-1990 growing season was also unique (Krenzer et al., 1990) in that no rainfall occurred in November and December 1989, and in early January, 1990, resulting in drought stress conditions. Rainfall resumed in mid-January, 1990 and did not cease until May. In contrast, during the selection year (1987-1988) conditions for forage production during fall of 1987 were unusually good while cold soils and snow cover in much of the second half of December, all of January and early February, 1988 resulted in no growth of wheat (Krenzer et al., 1988). This was an unusually long dormant period for wheat in Oklahoma.

Although final selection of HF and LF groups for this study was made only on the basis of total forage index values, greater separation was found between selection groups for the fall component than the winter component (Table 1). We practiced truncation selection only for total forage capacity to limit selections to a feasible number yet consider both seasonal components.

In the first year of testing (1988-1989), significant differences were found among entries for total forage yield, fall forage yield, and winter forage yield including their long-term and short-term components (Table 2). Variation among entries was partitioned into components corresponding to three checks, six parents, and the 36 selections. Thunderbird is noted in Oklahoma for its high forage yield in the fall, while TAM 200 is noted for its winter forage production immediately after breaking dormancy (Thompson, 1990). Thunderbird exceeded TAM 200 in total forage yield and fall forage production, but they did not differ in winter forage production (Tables 2 and 3). Blending those two cultivars did not result in a significant change in forage yield compared to the mean of each grown separately (data not shown). Parents differed significantly for most forage traits. Chisholm and Arkan showed the highest total forage yield (344 and 342 g m^{-2}, respectively), while OK79256 showed the lowest (234 g m^{-2}). Performance of a particular parent relative to others was not the same for fall and winter production. For example Pioneer 2165 produced 106 and 187 g m^{-2} in the fall and winter, respectively, while Arkan produced 175 and 167 g m^{-2}.

The 36 selections differed significantly for all measurements of forage production. Variation among selections was partitioned into variation among population means, among selection group means within populations, and among individual line means within selection groups and populations. Populations differed significantly for total forage yield and all indicators of winter forage yield. Population 2 (Pioneer 2165/Arkan) produced the highest total forage (302 g m^{-2}), and population 3 (OK79256/Arkan) produced the lowest (272 g m^{-2}). Selection groups differed significantly for most indicators of forage production,

except total winter forage yield and winter LT-2 forage yield. Examination of selection group means within each population revealed inconsistent responses throughout the growing season, particularly in population 1. The HF group in population 1 produced significantly more forage than the LF group in the fall; however, the reverse trend was observed in the winter, making total forage production statistically the same between groups (Table 3). In population 2, the HF group significantly out-yielded the LF group in total forage yield and all indicators of fall forage production. In contrast to population 1, a positive selection response was observed also in the winter, except for late winter forage yields. The winter LT-1 response was highly positive and larger than the sum of the negative responses of winter LT-2 and ST. Thus, the selection response for total winter production was positive (P<.10). In population 3, the HF group was again superior to the LF group for total forage and all indicators of fall production. Like population 1, this trend was not maintained in the winter. Examination of the mean index values for total forage and its fall and winter components showed that HF group produced significantly higher values than LF groups in all populations; differences were much higher for the fall component compared to the winter component (data not shown).

In the second year of forage testing at Perkins, OK (1989-1990), entries differed significantly (P<0.05) for total forage yield and all components of winter forage, but differences in fall forage were less pronounced (Table 4). Environmental conditions in second year favored TAM 200, as TAM 200 significantly outyielded Thunderbird for total forage yield, most indicators of fall forage production, and LT-2 forage

in the winter (Tables 4 and 5). Their blend again failed to show a significant change in forage yield compared to each check grown separately (data not shown). Parents did not differ significantly for most measurements of forage production except fall LT-2 and total winter forage. Arkan showed the highest total forage yield (379 g m^{-2}) and OK79256 showed the lowest (315 g m^{-2}). Variation among the 36 selections was significant for total forage yield, only LT-2 yield in the fall, and all indicators of winter forage production. Population means differed for the same traits, but with different ranking than the previous year. Population 1 (OK79257/Ok82377//Chisholm) produced the highest total forage yield (355 g m^{-2}) and population 2 (Pioneer 2165/Arkan) produced the lowest (315 g m^{-2}).

In population 1, the HF group significantly (P<0.01) outyielded the LF group in total forage yield, as well as all indicators of fall production except fall ST regrowth, but the two groups were similar in winter forage yields (Table 5). In population 2, the HF group was superior to LF group for total fall forage yield (P<.10) including the fall LT-1 component (P<.05), but the two groups were similar for LT-2 and ST fall components measured later in the season. Selection response in the winter was generally nonsignificant or negative for ST regrowth. These mixed responses led to no significant advantage in the HF group for total forage yield. In population 3, HF and LF groups were also similar for total forage yield, including most indicators of fall forage production. Selection responses were unexpectedly negative for winter forage yields (Table 5). Similar to the first year, the HF groups consistently had significantly higher mean index values than the LF

groups for total forage and its fall and winter components; but differences for the fall component were larger compared to winter component.

Visual selection was effective in sorting extreme differences in forage capacity, and these visual differences generally translated to different forage yields in fall. With one exception where HF and LF groups were equal, the HF groups were superior to the LF groups for fall forage production in the six population-year combinations. That superiority was generally not maintained for winter production except in population 2 in 1988-1989. Whenever the selection response for total winter forage was positive, a significant selection response was also observed in total forage yield. This occurred in three of the six population-year combinations. In populations and/or environments where winter production does not counteract fall production, improvement in total forage production will be feasible and high.

High forage producing lines were occasionally found in the LF groups and vice versa. For example in 1988-1989, an HF line in population 1 produced 227 g m^{-2} total forage while a LF line in the same population produced 336 g m^{-2}. Similarly in 1989-1990, an HF line in this population produced 340 g m^{-2} total forage while a LF line produced 366 g m^{-2} total forage. In 1989-1990, an HF line in population 3 produced 320 g m^{-2} total forage while a LF line produced 380 g m^{-2}. Similar examples were found in the other populations each year. In spite of such overlapping for total forage in few cases, no line in the LF groups produced higher forage than the highest forage producing line in HF groups in 1988-1989 in any population. The same was true for lines in populations 1 and 2 in 1989-1990 but in population 3, two lines in the LF group outyielded the highest line in HF group. In some cases

high forage producing lines in the LF group were classified as pros-trate.

Performance of selection groups was generally stable for fall forage but varied from year to year for winter forage and consequently for total forage production. This indicates that clipping trials of selected lines may be necessary in more than one environment. Thompson (1990) also reported that genetic differences in winter forage were more sensitive to environment while fall forage yields were relatively stable. He found no significant difference for late winter forage production of 18 winter wheat cultivars. He, therefore, suggested that fall forage capability appears more important. Huffine et al. (1960) reported that the period of forage production (fall, winter, or spring) for any small grain variety is just as important as total forage yield. Since producers who graze stocker cattle on wheat pasture frequently find that the amount of forage produced in the fall limits the stocking rate which wheat pastures can support (Thompson, 1990), the findings of this study complement the need to improve fall forage yield and thereby enhance the release of more efficient fall-forage producing cultivars. The extra forage produced could be used for hay when the wheat pasture is dormant or covered by snow.

No significant relationship (r=0.04, P>0.10, df=43 in 1988-1989; r=-0.03, P>0.10, df=43 in 1989-1990) was found between total fall and total winter forage yields among entry means. Thompson (1990) found a negative relationship between fall and winter forage yields, but Carver et al. (1991) found no significant relationship. Thompson (1990) also reported that fall forage yield was almost twice that of winter forage yield. However, yield differential was not quite so large in this study.

The combined analysis of variance over years for grain yield showed
no significant difference between HF and LF groups in any population in
the clipped plots (data not shown). In the conventional non-clipped
plots, the HF group was significantly higher yielding than the LF group
only in population 2 (P<0.10). Otherwise, selection groups did not
differ in grain yield. Significant differences were also observed among
lines within selection groups in populations 1 and 3. Grain yield of
clipped plots was reduced by 31% compared to grain yield of non-clipped
plots. Thompson (1990) also reported a 13 to 26% reduction in grain
yield, even though terminal meristems were not removed during clipping.
The correlation between grain yields under clipped and non-clipped
conditions was positive in both years (Table 6). Correlations between
total forage yield and grain yields under clipped or non-clipped
conditions were very low and nonsignificant. Atkins et al. (1969) also
reported no relationship between forage yield and grain yield in barley
and oats. These results show that selection for forage yield does not
produce a correlated response in grain yield. On the other hand, the
lack of negative correlation makes it possible to develop cultivars with
both high grain yield and high forage yield potential.

The positive responses to divergent selection indicate that visual
selection was effective in manipulating fall forage production. Further
efforts should be aimed at improving forage production potential prior
to winter dormancy. Success in improving forage yield, however, does
not guarantee the same for grain yield.

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Table 1. Mean index values of groups of six lines selected within three populations near Stillwater, OK, in 1987-1988.

Population	Pedigree	Selection group[+]	Total-forage index[‡]	Fall component	Winter component
1	OK79257/OK82377//Chisholm	High	4.00	2.50	1.50
		Low	-7.83	-4.83	-3.00
2	Pioneer 2165/Arkan	High	1.92	1.00	0.92
		Low	-9.59	-4.42	-5.17
3	OK79256/Arkan	High	3.17	2.50	0.67
		Low	-8.41	-5.08	-3.33

+ Selection based on either high or low values of the total forage index within each population.

‡ Total-forage index for each entry produced by summing the scores of fall and winter components.

Table 2. Selected mean squares for total, fall, and winter forage yields (g m^{-2}) of checks, parents, and selection groups in three wheat populations near Perkins, OK, in 1988-1989.

Source	df	Total forage	Fall forage‡			Winter forage‡			
			Total	LT	ST	Total	LT-1	LT-2	ST
Entries	44	6,163**	2,455**	1,768**	136*	3,471*	1,702*	345*	591**
TAM 200 vs. Thunderbird	1	14,340**	17,708**	13,064**	353*	177	2	60	49
Parents	5	9,964*	4,062*	3,034*	123	2,826	1,040	193	622*
Selections	35	5,470*	1,897**	1,333**	140*	3,670*	1,913*	334+	646**
Populations (P)	2	11,258*	231	268	8	12,489*	6,398*	864*	1,102*
Selection groups (SG)/P	3	15,967*	8,862**	5,792**	354**	4,177	6,362*	235	793*
Lines/SG/P	30	4,034	1,312*	958*	128+	3,032+	1,170	309	601*
Error	132	3,527	798	601	90	2,176	1,106	224	225

+, *, ** Significant at P = .10, .05, and .01, respectively.

‡ LT = Long-term forage yield;   ST = Short-term forage yield.

Table 3. Means for total, fall, and winter forage yields of selection groups and checks in three wheat populations near Perkins, OK, in 1988-1989.

Population	Selection group	Total forage	Fall forage‡			Winter forage‡			
			Total	LT	ST	Total	LT-1	LT-2	ST
					$g\ m^{-2}$				
1	High	295	124	90	34	171	90	40	41
	Low	291	99**	69**	30	192	99	47	46
	Response§	4	25	21	4	-21	-9	-7+	-5
2	High	328	130	95	35	198	111	40	47
	Low	275**	100**	73**	27**	175	74**	41	60**
	Response	53	30	22	8	23+	37**	-1	-13**
3	High	288	128	94	34	160	78	35	47
	Low	255*	102**	72**	30	153	69	35	49
	Response	33	26	22	4+	7	9	0	-2
Checks	TAM 200	272	84	58	26	188	83	52	53
	Thunderbird	356	178	139	39	178	84	46	48

+, *, ** Significant at P = .10, .05, and .01, respectively.

‡ LT = Long-term forage yield; ST = Short-term forage yield.

§ Response = Mean of high selection group - Mean of low selection group.

Table 4. Selected mean squares of total, fall, and winter forage yields ($g\ m^{-2}$) of checks, parents, and selection groups in three wheat populations near Perkins, OK, in 1989-1990.

Source	df	Total forage	Fall forage‡				Winter forage‡			
			Total	LT-1	LT-2	ST	Total	LT-1	LT-2	ST
Entries	44	4,710*	2,348	787	1,214**	262	2,520**	374*	643**	531**
TAM 200 vs. Thunderbird	1	11,409*	4,745*	26	4,071*	815+	1,439	382	2,051*	723*
Parents	5	1,813	2,563	701	1,549+	322	1,429+	205	480	51
Selections	35	5,187*	2,402	731	1,044*	201	2,806**	381*	670**	631**
Populations (P)	2	19,999**	2,501	26	2,398*	95	22,181**	2,163**	4,739**	1888**
Selection groups (SG)/P	3	8,511*	7,404*	2,264*	1,567+	329	1,894+	180	616+	285+
Lines/SG/P	30	3,867	1,895	625	901	195	1,605**	282	404+	581*
Error	132	3,073	1,969	741	710	283	749	229	283	121

+, *, ** Significant at P = .10, .05, .01, respectively.

‡ LT = Long-term forage yield; ST = Short-term forage yield.

Table 5. Means for total, fall, and winter forage yields of selection groups and checks in three wheat populations near Perkins, OK, in 1989-1990.

Popu-lation	Selection group	Total forage	Fall forage‡				Winter forage‡			
			Total	LT-1	LT-2	ST	Total	LT-1	LT-2	ST
						g m^{-2}				
1	High	375	188	84	104	59	187	44	63	80
	Low	335**	159*	71*	88	55	176	43	56	77
	Response§	40	29*	13*	16+	4	11	1	7	3
2	High	325	184	84	100	55	141	32	41	68
	Low	304	160	68*	92	53	144	29	40	75*
	Response	21	24+	16*	8	2	-3	3	1	-7*
3	High	339	170	82	88	59	169	35	51	83
	Low	338	151	71	80	51*	187	41	61	85
	Response	1	19	11	8	8*	-18+	-6	-10+	-2
Checks	TAM 200	388	201	62	139	79	187	49	72	66
	Thunderbird	312	152	58	94	59	160	35	40	85

+, * Significant at P = .10, and .05, respectively.

‡ LT = long-term forage yield; ST = Short-term forage yield.

§ Response = Mean of high selection group - Mean of low selection group.

Table 6. Correlations between grain yield in clipped and non-clipped plots and with forage yield among 45 wheat genotypes.

Year		Grain yield (non-clipped)	Forage yield
1988-1989	Grain yield (clipped)	0.39^{**}	0.24
	Grain yield (non-clipped)		0.12
1989-1990	Grain yield (clipped)	0.39^{**}	-0.05
	Grain yield (non-clipped)		-0.13

** Significant at $P = .01$; df = 43.

2

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