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PREVIEW

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**Chromosomal locations of quantitative trait loci affecting  
agronomic performance and environmental stability of seven  
traits of the Cheyenne-Wichita wheat chromosome substitution  
series**

Berke, Terry Glenn, Ph.D.

The University of Nebraska - Lincoln, 1990

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PREVIEW

**CHROMOSOMAL LOCATIONS OF QUANTITATIVE TRAIT LOCI AFFECTING  
AGRONOMIC PERFORMANCE AND ENVIRONMENTAL STABILITY OF SEVEN TRAITS  
OF THE CHEYENNE-WICHITA WHEAT CHROMOSOME SUBSTITUTION SERIES**

by

Terry Glenn Berke

A Dissertation

Presented to the Faculty of  
The Graduate College in the University of Nebraska  
In Partial Fulfillment of Requirements  
For the Degree of Doctor of Philosophy

Major: Agronomy

Under the Supervision of Professor P.S. Baenziger

Lincoln, Nebraska

August, 1990

DISSERTATION TITLE

Chromosomal Locations of Quantitative Trait Loci Affecting Performance and

Stability of the Cheyenne-Wichita Wheat Chromosome Substitution Series

BY

Terry Glenn Berke

SUPERVISORY COMMITTEE:

APPROVED

DATE

P. Stephen Baenziger  
Signature

8/6/90

P. Stephen Baenziger  
Typed Name

M. Rosalind Morris  
Signature

8/6/90

M. Rosalind Morris  
Typed Name

C. James Peterson  
Signature

8/6/90

C. James Peterson  
Typed Name

Kenneth P. Vogel  
Signature

8/6/90

Kenneth P. Vogel  
Typed Name

Dermot P. Coyne  
Signature

8/6/1990

Dermot P. Coyne  
Typed Name

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Signature

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Typed Name



GRADUATE COLLEGE  
UNIVERSITY OF NEBRASKA

**CHROMOSOMAL LOCATIONS OF QUANTITATIVE TRAIT LOCI AFFECTING  
AGRONOMIC PERFORMANCE AND ENVIRONMENTAL STABILITY OF SEVEN TRAITS  
OF THE CHEYENNE-WICHITA WHEAT CHROMOSOME SUBSTITUTION SERIES**

Terry Glenn Berke, Ph.D.

University of Nebraska, 1990.

Advisor: P.S. Baenziger

A major limitation to the genetic improvement of wheat is the lack of information on genes that affect agronomic performance and environmental stability of quantitative traits. This study had two objectives: (1) to determine which chromosomes carry quantitative trait loci (QTLs) affecting agronomic traits in wheat, including grain yield ( $\text{Mg ha}^{-1}$ ), seeds tiller<sup>-1</sup>, 1000 seed weight (g), tillers  $\text{m}^{-2}$ , grain test weight ( $\text{kg m}^{-3}$ ), plant height (cm), and anthesis date; and (2) to determine which chromosomes have QTLs affecting the environmental stability of these traits.

The materials for this study were reciprocal sets of chromosome substitution lines developed in duplicate at the University of Nebraska between two hard red winter wheat cultivars, Cheyenne and Wichita. The lines were evaluated in field trials conducted in 1987 at Lincoln [Typic Argiudoll soil], in 1988 at Lincoln, Mead, [Typic Argiudoll soil], and Alliance [Aridic Argiustoll soil], and in 1989 at Lincoln, Mead, Alliance, and North Platte, NE [Typic Argiustoll soil], using a randomized complete block design with three replications at each site.

We detected QTLs on Wichita chromosomes 3A and 6A that significantly increased grain yield in Cheyenne, and on Cheyenne chromosomes 3A and 6A that significantly decreased grain yield in Wichita. We detected QTLs that affected each of the other traits on one or more chromosomes.

Homoeologous group 3 chromosomes carried proportionately more QTLs than other homoeologous groups.

Data from 74 substitution lines and the two parents grown in six environments were used to compute stability parameters ( $b_i$ ,  $s^2_e$ , C.V.). We detected QTLs on Wichita chromosomes 3A, 6A, 2B, and 3D that decreased the environmental stability of grain yield in Cheyenne, and on Cheyenne chromosome 1D that increased the environmental stability of grain yield in Wichita. We detected QTLs on one or more chromosomes that affected environmental stability of each of the other traits except plant height. No homoeologous group of chromosomes carried proportionately more QTLs affecting environmental stability of these traits.

PREVIEW



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Special thanks to my wife, Sarah, whose love, support, and encouragement were instrumental in the completion of this dissertation.

This thesis is dedicated to my Lord and Savior Jesus Christ.

"For God so loved the world that He gave His one and only Son, that whoever believes in Him will not die, but have eternal life"

John 3:16

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## FOREWORD

This dissertation is written as two manuscripts in the format required for contributors to Crop Science, plus a general introduction and general summary.

PREVIEW

## GENERAL INTRODUCTION

Wheat is a crop of global economic importance. World production of wheat in 1989 was estimated at 535 million metric tons (Anonymous, 1990 on p.93). On a global basis, wheat provides more nourishment for people than any other food source (Johnson et al., 1978). Most wheat is consumed by humans in the form of bread, pasta, semolina, etc. If world food consumption grows 2% annually as projected over the next 15 years, wheat demand will rise by nearly one-third (Brown, 1987). By the year 2020, feeding the world's projected 7.8 billion people will require average grain yields 56% higher than at present (Wolf, 1987). Production of wheat can increase primarily in three ways: (i) devote more hectares of land to wheat production, (ii) use more intensive management practices (fertilizers, herbicides, pesticides, irrigation, mechanization, etc.), and (iii) manipulate wheat genetically to produce higher yields.

The first alternative has limited returns; most of the fertile land in the world is under tillage already, and marginal lands are generally vulnerable to wind and water erosion (Brown and Postel, 1987). Shifting wheat to land previously used to produce other foodstuffs may increase world food production, but only marginally.

The second alternative has limited returns also; the increased production may be offset by its cost in terms of money and damage to the environment. Intensive management practices tend to be capital- and energy-intensive. Many Third World farmers cannot afford costly machinery and fertilizers (Brown, 1987). Application of high levels of nitrogen fertilizer may result in pollution by nitrate leaching into

surface and underground water supplies (Huber et al., 1977).

The third alternative offers potentially large returns in terms of time and energy invested. Wheat can be improved genetically by breeding for disease and insect resistance, drought resistance, lodging resistance, and improved agronomic performance, resulting in higher grain yields without changing agronomic practices. Cox et al. (1988) estimated in Kansas a genetic gain in grain yield of hard red winter wheat of 1% year<sup>-1</sup> from 1919 to 1987. Once an improved wheat cultivar is developed, it can be multiplied for distribution over large areas since wheat is a self-pollinated species.

A major limitation to the genetic improvement of wheat is the lack of knowledge about the genes that control grain yield and its components, seeds tiller<sup>-1</sup>, seed weight, and tillers m<sup>-2</sup>, as well as other important agronomic traits such as grain test weight, plant height, and anthesis date. These traits are presumed to be controlled by numerous genes, each of which has small effects (hence indistinguishable) which are often modified by the environment in which the plant is grown. This produces continuous phenotypic variation rather than discrete phenotypic classes. Historically, these traits have been termed quantitative traits, and the loci of the genes affecting them are commonly referred to as quantitative trait loci (QTLs) (one locus = QTL). Quantitative geneticists have primarily concentrated on developing statistical models to describe types of gene action as additive, dominant, and epistatic.

A number of methods for locating specific QTLs responsible for quantitative genetic variation have been proposed. Qualset (1979) suggested developing a series of pure lines via single seed descent

(SSD) to represent the fixable continuous phenotypic variation of a cross. Phenotypically similar SSD lines could be intermated. If they also are genotypically near-identical (similar), progeny from such a cross may segregate for the few genes that are different in the parents. With a precise assay, the progeny may show simple Mendelian segregation ratios for quantitative traits.

A second method (Robertson, 1985) uses transposon tagging to clone genes for a distinct phenotypic trait, such as waxy endosperm, in order to locate different "wild-type" alleles at the same locus. Small phenotypic differences for the trait could be explained by sequence variations in the "wild-type" allele or its regulatory sequences. This method assumes that there is sequence homology between the phenotypically distinct allele and the "wild-type" alleles. However, this would not be possible if the trait were due to a complete deletion of the "wild-type" allele.

A third method (Snape et al., 1983) involves backcross reciprocal monosomic analysis. By making appropriate crosses and backcrosses with monosomics, pairs of whole chromosomes and the genes thereon can be isolated in an average, though heterozygous and heterogeneous, background. A series of lines representing each chromosome pair is tested to determine the average effect of that chromosome. However, this method is limited to species that will tolerate monosomics.

A fourth method (Helentjaris et al., 1985; Lander and Botstein, 1989) uses restriction enzymes to map "markers" on chromosomes by comparing DNA variation between two different cultivars. These markers, termed restriction fragment length polymorphisms (RFLPs), can

be followed in the progeny resulting from a cross of the two cultivars to determine if they are associated with a particular trait, such as fruit size. Sufficient DNA variation must exist between two cultivars to obtain a large set of polymorphic "markers". Many chromosome markers are needed to create an RFLP map dense enough to isolate and clone a QTL (Meyerowitz and Pruitt, 1985).

A fifth method (Wehrhahn and Allard, 1965) uses a series of "inbred backcross" lines to fix the quantitative variation for a trait and determine the number of QTLs responsible for a trait. This method utilizes simple breeding techniques and is available to a large number of crop species. However, in the absence of discontinuities in the distribution of inbred backcross line means, the inbred-backcross technique is incapable of distinguishing between a relatively simple genetic interpretation and one based on the presence of many genes each of small effect.

A sixth method (Law, 1966) is to use chromosome substitutions between cultivars to study the effect of a chromosome pair in a common, homozygous background. One-way substitutions (each chromosome of one cultivar is substituted separately for its homologue in another cultivar) have been used to establish QTL-chromosome associations for many quantitative traits (Ausemus et al., 1967; Morris, 1960-1984; Sasaki et al., 1968; Law and Worland, 1973; Sasaki et al., 1973; Doekes and Belderok, 1976; Giorgi et al., 1978; Sutka, 1981; and Mansur et al., 1990).

The limitations of one-way chromosome substitutions in determining between-chromosome interactions can be overcome by using two-way or

reciprocal substitutions between two cultivars (Law, 1966). Complete reciprocal chromosome substitution series between two cultivars are rare because of the cytological expertise and time required to develop them.

The reciprocal substitution series between two hard red winter wheat cultivars, Cheyenne and Wichita, developed by Dr. M.R. Morris, has been used to establish QTL-chromosome associations for anthesis date (Zemetra et al., 1986). Wichita carried major QTLs affecting heading date on chromosomes 3A and 3D, while Cheyenne carried major QTLs on 3A, 6A, and 3D. The QTLs from Wichita accelerated heading in Cheyenne, and the QTLs from Cheyenne delayed heading in Wichita.

The reciprocal substitution series between Cheyenne and Wichita has also been used to establish QTL-chromosome associations for winter-hardiness and vernalization (Zemetra and Morris, 1988). Wichita carried one QTL affecting winterhardiness and vernalization on chromosome 3B. This gene is unique from other previously reported winterhardiness genes because its expression is dominant in Cheyenne but suppressed in Wichita.

The reciprocal substitution series between Cheyenne and Wichita has also been used to establish QTL-chromosome associations for traits associated with lodging (Al-Qaudhy et al., 1988), including straw strength, height, length and diameter of basal internodes, number and width of inner vascular bundles, width of culm wall, diameter of culm cavity, and width of tissue from epidermis through sclerenchyma layer. Wichita appeared to carry major QTLs affecting straw strength on chromosomes 3A and 1D, while Cheyenne carried major QTLs on chromosomes 6A, 3B, and 5D. Cheyenne chromosomes 6A and 3B each produced favorable



effects in Wichita on several traits related to lodging resistance. Substitutions of Cheyenne chromosomes into Wichita produced approximately three times as many significant phenotypic changes as substitutions of Wichita chromosomes into Cheyenne.

The reciprocal substitution series between Cheyenne and Wichita has also been used to establish QTL-chromosome associations for flour and protein quality (Zemetra et al., 1987). Wichita carried major QTLs affecting flour mixing time on chromosome 1B, while Cheyenne carried major QTLs on chromosomes 1B, 3B, and 2D. The QTLs from Wichita decreased mixing time in Cheyenne, and the QTLs from Cheyenne increased mixing time in Wichita. Flour relative mixing tolerance was also measured; Wichita did not carry any major QTLs affecting flour mixing tolerance, while Cheyenne carried major QTLs on chromosomes 1B, 3B, and 7B. The QTLs from Cheyenne increased relative flour mixing tolerance.

Despite the information obtained by the various methods on QTLs that affect quantitative traits, little is known about QTLs that control stability of quantitative traits. This is primarily due to the extensive multi-environment testing required to measure environmental stability. The concept of stability is ambiguous and depends on how it is defined. Lin et al. (1986) defined three concepts of stability: 1) A genotype is considered to be stable if its variance among environments is small; 2) A genotype is considered to be stable if its response to environments is less than or parallel to the mean response of all genotypes in the trial; and 3) A genotype is considered stable if the residual MS from the regression model in the environmental index is small.

An example of a Type 1 stability parameter is the coefficient of variation (C.V.), an example of a Type 2 stability parameter is the regression coefficient (b) on the environmental index, and an example of a Type 3 stability parameter is the deviations from regression ( $s^2_d$ ) of a genotype on the environmental index. For this dissertation, the stability parameters measured were the coefficient of variation (C.V.), regression coefficient (b) on the environmental index, and the deviations from regression ( $s^2_d$ ).

Stability of quantitative traits in wheat has been presumed to be controlled by numerous QTLs, each of which has small effects. Wheat cultivars, as well as wheat hybrids, are known to differ genetically for their stability across different environments. Mahal et al. (1988) studied 12 parents and 48 F<sub>1</sub> hybrids from the parents. They found significant differences for stability of grain yield and yield components among both parents and hybrids. Changes in stability of yield components were also found among parents and among their hybrids.

Carver et al. (1987) studied hybrids, semi-dwarf cultivars, and tall cultivars. They found that hybrids and semi-dwarf cultivars tended to be less stable (higher b value), while tall cultivars tended to be more stable. Sharma et al. (1987) found that wheat cultivars and hybrids differed in stability of both harvest index and yield, and there was no correlation between the two traits.

Rajaram et al. (1983) examined cultivars with and without the 1B/1R translocation and found that cultivars with the 1B/1R translocation tended to be less stable (higher b value) than cultivars without the 1B/1R translocation. Gill et al. (1984) measured stability of wheat

multilines differing in stripe rust resistance (incited by *Puccinia striiformis* West. var. *striiformis*). They found that one of four multilines was less stable (higher b value) than the recurrent parent. It had superior stripe rust resistance and performed well in high-yielding environments.

Previous reports on environmental stability of agronomic traits in wheat have examined different genotypes such as pure-line cultivars, multi-line cultivars, and hybrids. No attempt was made to detect QTLs responsible for the stability response observed. Genetic analyses of quantitative traits in wheat have been greatly facilitated by chromosome substitution lines. However, a study of reciprocal chromosome substitution lines to detect QTLs for performance and stability of important agronomic traits such as grain yield, seeds tiller<sup>-1</sup>, 1000 seed weight, tillers m<sup>-2</sup>, grain test weight, plant height, and anthesis date has not been reported. This is presumably because the substitution lines were tested in relatively few environments (generally three or less).

The objectives of this study were as follows:

(1) to determine which chromosomes carry QTLs affecting important agronomic traits such as grain yield, seeds tiller<sup>-1</sup>, 1000 seed weight, tillers m<sup>-2</sup>, grain test weight, plant height, and anthesis date; and

(2) to determine which chromosomes carry QTLs affecting the environmental stability of grain yield, seeds tiller<sup>-1</sup>, 1000 seed weight, tillers m<sup>-2</sup>, grain test weight, and plant height.

**PART I**  
**CHROMOSOMAL LOCATIONS OF QUANTITATIVE TRAIT LOCI AFFECTING AGRONOMIC**  
**PERFORMANCE OF THE CHEYENNE-WICHITA CHROMOSOME SUBSTITUTION SERIES**

PREVIEW

### ABSTRACT

A major limitation to the genetic improvement of wheat (*Triticum aestivum* L.) is the lack of information about quantitative trait loci (QTLs). The objective of this study was to determine the chromosomal locations of QTLs controlling the following important quantitative traits: grain yield, seeds tiller<sup>-1</sup>, 1000 seed weight, tillers m<sup>-2</sup>, grain test weight, plant height, and anthesis date. Reciprocal sets of chromosome substitution lines in duplicate between two hard red winter wheat cultivars, Cheyenne and Wichita, were used to identify the chromosomes. Field trials using a randomized complete block design with three replications were conducted in 1987 at Lincoln [Typic Argiudoll soil], in 1988 at Lincoln, Mead, [Typic Argiudoll soil], and Alliance [Aridic Argiustoll soil], and in 1989 at Lincoln, Mead, Alliance, and North Platte, NE [Typic Argiustoll soil].

Wichita had major QTLs on chromosomes 3A and 6A that increased grain yield in Cheyenne and major QTLs on chromosome 3B that decreased grain yield in Cheyenne, while Cheyenne had major QTLs on chromosomes 3A and 6A that decreased grain yield in Wichita. The increase in grain yield by Wichita chromosomes 3A and 6A was due to a significant ( $P < 0.05$ ) increase in 1000 seed weight. The decrease in grain yield by Cheyenne chromosomes 3A and 6A was due to a significant ( $P < 0.05$ ) decrease in tillers m<sup>-2</sup>. The decrease in grain yield by Wichita chromosome 3B was due to a significant decrease in winterhardiness, resulting in decreased 1000 seed weight and tillers m<sup>-2</sup>. We identified one Wichita and seven Cheyenne chromosomes with QTLs affecting seeds tiller<sup>-1</sup>. We identified seven Wichita and five Cheyenne chromosomes with QTLs affecting 1000 seed weight. We identified one Wichita and three Cheyenne chromosomes with QTLs affecting tillers m<sup>-2</sup>. We identified one or more chromosomes with QTLs affecting each of the other agronomic traits. Further study of chromosomes 3A and 6A via recombinant chromosome lines is in progress.

## INTRODUCTION

A major limitation to the genetic improvement of wheat is the lack of specific information about quantitative trait loci (QTLs) (one locus - QTL) that control quantitative traits such as grain yield and its component traits (seeds tiller<sup>-1</sup>, 1000 seed weight, tillers m<sup>-2</sup>), grain test weight, plant height, and anthesis date. Quantitative traits have been presumed to be controlled by numerous genes, each of which has small effects, and whose action is often modified by the environment (Falconer, 1981). A number of methods for studying quantitative trait variations have been proposed, including chromosome substitution lines (Law, 1966), intermating single seed descent (SSD) lines (Qualset, 1979), backcross reciprocal monosomic analysis (Snape et al., 1983), inbred-backcross lines (Wehrhahn and Allard, 1965), and RFLP mapping (Helentjaris et al., 1985; Lander and Botstein, 1989). Of these methods, RFLP mapping holds the greatest promise for isolating and cloning a QTL, although a dense RFLP map is needed to be able to clone a gene (Meyerowitz and Pruitt, 1985). The other methods require lengthy germplasm development, segregating materials that confound year effects with inbreeding, or genetic techniques (i.e. transposon tagging, Robertson, 1985) not currently available in wheat.

Genetic analyses of hexaploid wheat traits have been facilitated by chromosome substitution lines (Law, 1966). One-way substitutions (each chromosome of one cultivar is substituted separately for its homologue in another cultivar) have been used to establish chromosome associations for many quantitative traits such as cold resistance, baking quality, quantity and quality of kernel proteins, and maturity (Ausemus et al., 1967; Morris, 1960-1984; Sasaki et al., 1968; Law and Worland, 1973; Sasaki et al., 1973; Doekes and Belderok, 1976; Giorgi et al., 1978; Sutka, 1981; Mansur et al., 1990). The limitations of one-way chromosome substitutions in determining between-chromosome interactions against uniform genetic backgrounds can be overcome by using reciprocal

or two-way substitutions between two cultivars (Law, 1966). Complete reciprocal chromosome substitution series are rare because of the cytological expertise and time required to develop them. However, in crops such as wheat and maize (*Zea mays* L.), efficient use of chromosomal manipulations can foster RFLP studies (Kam-Morgan et al., 1989; Weber and Helentjaris, 1989).

The reciprocal chromosome substitution series between two hard red winter wheat cultivars, Cheyenne and Wichita, has been used to establish QTL-chromosome associations for anthesis date (Zemetra et al., 1986), winterhardiness and vernalization (Zemetra and Morris, 1988), flour and protein quality (Zemetra et al., 1987) and traits associated with lodging (Al-Qaudhy et al., 1988).

Because of the importance of grain yield and other agronomic traits, the objectives of this study were to determine the chromosomal locations of QTLs affecting quantitative traits, including grain yield and its component traits (seeds tiller<sup>-1</sup>, 1000 seed weight, and tillers m<sup>-2</sup>), grain test weight, and plant height, and to confirm anthesis date observations made previously using the reciprocal chromosome substitutions between Cheyenne and Wichita.

## MATERIALS AND METHODS

The materials for this study were reciprocal sets of chromosome substitution lines developed by M.R. Morris at the University of Nebraska between two hard red winter wheat cultivars, Cheyenne and Wichita. These cultivars have been used extensively in crosses to develop hard red winter wheats for the Great Plains region. The development of the substitution lines was described by Zemetra et al. (1986). For each of the 21 chromosomes in the reciprocal sets, duplicate lines were developed to determine if the number of backcrosses was sufficient to achieve a uniform genetic background (Law and Worland, 1972). Hence a total of 84 lines and two parents would represent a complete reciprocal chromosome substitution set (in duplicate). One of the duplicate lines for Cheyenne chromosome 2B and one of the duplicate lines for Cheyenne chromosome 3B were not tested due to an insufficient number of backcrosses at the time of this study. All other lines had six or seven backcrosses except one of the duplicates of Cheyenne 7D into Wichita, which had five backcrosses.

Due to insufficient seed amounts, only 60 substitution lines and the two parental cultivars were grown in 1987 at the University of Nebraska Agronomy Research Farm near Lincoln, NE (Sharpsburg silty clay loam, a fine, montmorillonitic, mesic Typic Argiudoll). In 1988, 90 substitution lines and the parental cultivars were grown at Lincoln, 74 substitution lines and the parental cultivars were grown at the University of Nebraska Agricultural Research Center near Mead, NE (Sharpsburg silty clay loam, a fine, montmorillonitic, mesic Typic Argiudoll), and 69 substitution lines and the parental cultivars were grown at the Northwest Agricultural Laboratory near Alliance, NE (Keith loam, a fine-silty, mixed, mesic Aridic Argiustoll). In 1989, 90 substitution lines and the parental cultivars were grown at Lincoln, Mead, Alliance, and the University of Nebraska Research Center near North Platte, NE (Holdrege silt loam, a fine-silty, mixed, mesic Typic Argiustoll) (eight