Understanding Grain Yield: It Is a Journey, Not a Destination

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Abstract: Approximately 20 years ago, we began our efforts to understand grain yield in winter wheat using chromosome substitution lines between Cheyenne (CNN) and Wichita (WI). We found that two chromosome substitutions, 3A and 6A, greatly affected grain yield. CNN(WI3A) and CNN(WI6A) had 15 to 20% higher grain yield than CNN, whereas WI(CNN3A) and WI(CNN6A) had 15 to 20% lower grain yield than WI. The differences in grain yield are mainly expressed in higher yielding environments (e.g. eastern Nebraska) indicating genotype by environment interactions (G × E). In studies using hybrid wheat, the gene action for grain yield on these chromosomes was found to be mainly controlled by additive gene action. In subsequent studies, we developed recombinant inbred chromosome lines (RICLs) using monosomics or doubled haploids. In extensive studies we found that two regions on 3A affect grain yield in the CNN(RICLs-3A) with the positive QTLs coming from WI. In WI(RICLs-3A), we found a main region on 3A that affected grain yield with the negative QTL coming from CNN. The 3A region identified using WI(RICLs-3A) coincided with one of the regions previously identified in CNN(RICLs-3A). As expected the QTLs have their greatest effect in higher-yielding environments and also exhibit QTL × E. Using molecular markers on chromosomes 3A and 6A, the favorable alleles on 3A in Wichita may be from Turkey Red, the original hard red winter wheat in the Great Plains and presumably the original source of the favorable alleles. Cheyenne, a selection from Crimea, did not have the favorable alleles. In studying modern cultivars, many high yielding cultivars adapted to eastern Nebraska have the WI-allele indicating that it was selected for in breeding higher yielding cultivars. However, some modern cultivars adapted to western Nebraska where the QTL has less effect retain the CNN-allele, presumably because the allele has less effect (is less important in improving grain yield). In addition many modern cultivars have neither the WI-allele, nor the CNN-allele indicating we have diversified our germplasm and new alleles have been brought into the breeding program in this region.

Keywords: breeding; genetics; molecular markers; *Triticum aestivum* L.; wheat

The most important challenge facing plant breeders is how to effectively breed for increased grain yield. Obviously grain yield is a complex trait that is affected by the genotype (G), the environment (E), and the genotype by environment interaction (G × E). Due to its complexity, there is little information on the genes that affect this trait and what information there is, is often contradictory. However, the two most common models for complex traits can be summarized as: (1) Grain yield is controlled by numerous genes, each of which has a small effect and are virtually indistinguishable from each other, or (2) grain yield may be affected by fewer genes, some of which have relatively larger effects that can be identified by modern methods of genetic analysis (e.g. Buckler *et al.* 2009). As grain yield has considerable G × E, a second concern is that many of the alleles that were previously identified using molecular markers, often have not been confirmed in other populations. Basically, it is easier to find a QTL once than it is to find it twice (Bernardo 2008). However, all phenotypic, traits are controlled by genes and their interactions (epistatisis), the environment, and the G × E. Our goal was to better understand the genetics of grain yield.

When we began this research in the late 1980's, there were very few molecular markers and the tools that were being successfully applied to maize (*Zea mays* L.) were generally not available in wheat (*Triticum aestivum* L.) However, wheat researchers had excellent genetic materials in chromosome substitution lines that could partition the wheat genome one chromosome at a time, thus removing much of the complexity and much of the epistatic interactions. While many of these chromosome substitution lines were in Chinese Spring, a line totally unsuitable for realistic or representative grain yield evaluations, the Chinese Spring monosomics series had lead to the development of chromosome substitution series of agronomic importance. In Nebraska, Cheyenne was the founding cultivar that formed the basis of our germplasm for wheat cultivar development. Dr. Rosalind Morris developed a reciprocal chromosome substitution series of Cheyenne with Wichita a popular cultivar developed in Kansas. The coefficient of parentage of Cheyenne with then popular wheat cultivars Scout 66, Centurk, Brule, and Siouxland was 0.376, 0.408, 0.157, and 0.431, respectively (Cox *et al.* 1985). These cultivars have become key parents for many new wheat cultivars. Hence the reciprocal substitution lines were ideally suited to begin understanding grain yield. Furthermore, Cheyenne was a long term check in the Nebraska Intrastate Nursery, so that there was considerable data on its performance over time.

Hence our studies began by evaluating the reciprocal substitution series. In this paper, the background cultivar Cheyenne will be abbreviated as CNN and Wichita as WI. The substitution lines will be CNN(WI1A) where chromosome 1A from WI was substituted for 1A from CNN. Similarly WI(CNN7D) denotes WI where chromosome 7D from CNN was substituted for WI chromosome 7D. Though CNN was a popular and widely grown cultivar, over time it had lost some of its disease resistance, as had WI. Hence to avoid confounding effects of diseases, the trials were sprayed with fungicides and yield "potential" was actually measured. The fungicides controlled the major diseases that are commonly present in Nebraska and we were fortunate that the diseases that they did not control (e.g. viruses such as soilborne wheat mosaic virus, barley yellow dwarf virus, and wheat streak mosaic virus; and *Fusarium* spp.) were not present in these trials.

Identifying the chromosomes of interest

Our first goal was to identify the chromosomes of importance. To do this Berke *et al.* (1992a) evaluated the reciprocal chromosome lines in the major ecological zones of Nebraska (Peterson 1992). Because the lines were developed by backcrossing, each substitution line was made in duplicate with the understanding that any random effect due to backcrossing of importance could be measured by comparing the duplicate lines for the same substitution. In general, most duplicate lines were similar within the experimental error of the traits we measured. Their similarity was later confirmed using DArT markers by Dr. Rustgi. Hence, though there were 21 chromosome substitution lines for each background (21 for CNN and 21 for WI), Berke *et al.* (1992a), actually evaluated 84 + substitution lines due to some were at different levels of backcrossing, and most were BC_6. In this research, chromosomes 3A and 6A were found to be the two most important chromosomes affecting grain yield. CNN(WI3A) and CNN(WI6A) increased grain yield compared to CNN by 19% and 14%,

respectively, and WI(CNN3A) and WI(CNN6A) decreased grain yield compared to WI by 17% and 23%, respectively. CNN(WI3B) also greatly decreased grain yield, but this was due to reduced winter hardiness of CNN(WI3B). Evidently, there was a major gene(s) for winter survival on CNN3B that when replaced by WI3B, led to winterkilling. Interestingly the genes for winter survival in WI were not on WI3B, as WI(CNN3B) had the same winter survival as WI. Hence it appeared the beneficial genes on WI3A and WI6A were effective both in CNN and in WI. Similarly the detrimental effects of CNN3A and CNN6A were found in CNN and in WI. For ease of future work, we decided to work primarily on one chromosome, 3A. Because of the importance of CNN in the Nebraska wheat improvement effort, we chose CNN(WI3A) to study. We were fortunate in this choice as in this and the following 5 studies (discussed below) with 35 testing environments that included CNN and CNN(WI3A), CNN(WI3A) was always significantly better than CNN by an average of 14%. In Nebraska, G × E is very common and usually our coefficients of variation for research trials are between 10 and 15%, thus making it difficult to consistently find relatively small differences.

While the study of CNN(WI3A) was very important for understanding grain yield and the genes that control it, in retrospect there were other chromosomes that could have been studied that would help elucidate the genetics of grain yield. Berke *et al.* (1992b) studied the environmental stability of the substitution lines using procedures of Eberhart and Russell (1966). CNN(WI3A) yielded equal to or superior to CNN in all of the environments where it was tested. In general, in lower yielding environments (usually found in western Nebraska) CNN and CNN(WI3A) were similar, but in higher yielding environments CNN(WI3A) was consistently higher yielding. Hence the genes on WI3A were often beneficial and in some environments may have been neutral, but they were never detrimental. The genes on WI3A could be used without concern because they never hindered grain yield improvement in any environment.

If a breeder was interested in improving grain yield in low yielding environments, WI(CNN1D) increased grain yield compared to WI in low yielding environments, but reduced grain yield when compared to WI in high yielding environments (a classic crossover interaction; Haldane 1946; Russell *et al.* 2003). The mean over environments of WI (2.72 mg/ha) was very similar and not statistically different from WI(CNN1D) (2.71 mg/ha), but the response of the two lines to the environment was very different. Other chromosome substitution lines had similar means to their respective donor cultivar, but were very different in their response to the environment. We have not studied these lines further, but they could provide insight into G × E and how best to target lines for lower or higher yielding environments.

In a study to determine the gene action of the alleles on chromosome 3A, Yen *et al.* (1997) evaluated hybrids of CNN × WI, WI × CNN, CNN(WI3A) × CNN, CNN(WI6A) × CNN, WI(CNN3A) × WI, WI(CNN6A) × WI and found the genes acted in a largely additive fashion. A few hybrids had values near the higher yielding parent (indicating dominance), but there was no high parent heterosis identified in any hybrid. These results were expected as most gene action in wheat is additive and due to the difficulty in making the hybrids, there was limited seed for testing. Also, evaluating hybrids involving older, conventional height, lower yielding wheat cultivars is problematic due to limited heterosis and large coefficient of variation.

Breaking chromosomes – what have we learned?

Once we identified a chromosome that had a major effect on grain yield, we were very interested in determining if the chromosome contained numerous linked loci containing favorable alleles or a few major linked loci that contain major favorable alleles. To do this, we created recombinant inbred chromosome lines by making the cross CNN(WI3A) × CNN or its reciprocal cross and crossing the F_1 as a male parent to the CNN monosomic 3A (Kuspria & Unrau 1957; Law 1966;Yen & Baenziger 1992). By selecting the monosomic progeny, the recombinant chromosome could be isolated and upon selfing the progeny would either be monosomic or disomic for the recombinant inbred chromosome [hereafter designated CNN(RICL3A)]. In the first studies, Shah *et al.* (1999a, b) using 50 CNN(RICL3A)s, 13 molecular and one phenotypic markers (some of which cosegregated), and two to three replications identified QTLs for many agronomic traits, but not for grain yield over all environments.

Significant grain yield QTLs were found in a few environments, but they were at different loci in the environments. In retrospect, we had too few RICLs and too few molecular markers to identify small QTLs that exhibit considerable G × E. The population size of 50 RICLs, though small, in theory would have similar power to identify QTLs as 200 recombinant inbred lines (Kaeppler 1997). However, Kaeppler's estimations were based upon having 10 replications and a QTL accounting for 2.5% of the genetic variation with a heritability of 0.5.

In the next study, Campbell *et al.* (2003) used 95 unique CNN(RICL3A)s. Three additional RICLs were heterozygous, hence may have had a univalent shift and were not suitable for inclusion. In addition, the study used 20 molecular markers and an incomplete block design nested within four replications. The field design was chosen to improve the phenotypic measurements (Stroup *et al.* 1994) as a key part of the QTL discovery. The environments also tended to be split with more in eastern Nebraska or with higher grain yield where CNN(WI3A) tended to have greater grain yield than CNN. In this study, in the combined analysis and in three individual environments a significant grain yield QTL was identified. At a fourth environment, the QTL was nearly significant. In the environments where QTLs were identified, their grain yield tended to higher. In three additional environments, the QTL was not found. These environments tended to be lower yielding. Again, this highlighted the importance of G × E for grain yield and QTL by environment interactions. A minor QTL for grain yield was identified in a second segment of the chromosome. On the basis of this study, it looked as if grain yield improvement could be explained by two (one major and one minor) QTL on WI3A. As expected, both favorable alleles came from WI. Looking at the stability of the major QTL, it was clear that the WI allele had its greatest effect in the higher yielding environments when compared to the CNN allele. In the lower yielding environments, the WI and CNN alleles were similar in effect. Two other segments of 3A had QTLs affecting yield components (spikes per square meter, kernels per spike, and kernel weight). Identifying QTL affecting yield components that did not colocalize with grain yield QTL could either be due to compensation among yield components or it could indicate that grain yield is a much more difficult trait to measure than yield components. Overall, the additional lines, markers, and improved experimental field design (incomplete block designs with more replications) increased our statistical power and thus were critical to our identification of the QTLs.

The origin and use of the favorable QTLs from Wichita chromosome 3A

As the above mentioned QTLs have a major impact on grain yield, we were interested in which line was the source of the favorable QTL-alleles and have they been used in plant breeding. As a breeder, one would like to believe that if an allele was identified in their germplasm that could significantly increase grain yield that conventional breeding would have found and used the allele. Mahmood *et al.* (2004) using some of the SSR markers used by Campbell *et al.* (2003) and additional SSR markers looked at the molecular diversity of chromosome 3A in historic to modern wheat cultivars adapted to Nebraska. In using the three key polymorphic SSRs between CNN and WI for the main QTL identified by Campbell *et al.* (2003), they found three main clusters of the cultivars. The first cluster included CNN and many wheat cultivars adapted to western Nebraska where the CNN-allele was not different from the WI-allele for grain yield with a few notable exceptions (e.g., Wesley, a high yielding irrigated wheat cultivar). The second group included WI and many of the higher yielding modern cultivars. Turkey Red, the original hard red wheat brought to the Great Plains was clustered with WI in this group. Hence we believe that Turkey was the original source of the favorable allele(s) from WI that we have been studying. The third group had neither the CNN-, nor WI-allele indicating that new germplasm had been brought into the Great Plains as would be expected with the germplasm exchange occurring in modern wheat breeding programs. Hence, as would be expected, the favorable allele from WI appears to have been incorporated into modern wheat cultivars.

Interestingly, when looking at the 22 SSR markers that were polymorphic for chromosome 3A between CNN and WI, there again were three clusters for the lines. However, CNN and WI clustered in groups 1 and 3 and the remaining lines clustered between CNN and WI in group 2 indicating there were similarities among the whole chromosome 3A for the set of lines.

Understanding the phenology and environmental effects on grain yield

Grain yield is a complex trait that is the end result of many phenological aspects of plant growth and environmental inputs. Campbell *et al.* (2004) attempted to explain G × E and QTL × E interactions using factorial regression with environmental covariates, specifically solar irradiation, temperature, and precipitation before and during three phenological stages. The three stages were vegetative growth defined as from planting to terminal spikelet initiation, reproductive growth defined as terminal spikelet formation to anthesis, and grain filling period defined as anthesis to physiological maturity. In this research, G × E was able to be explained reasonably well by environmental covariates. For example, solar radiation during grain fill explained 23% of the G × E for grain yield. Similarly the role of solar radiation (22%) and temperature (18%) during vegetative growth, and precipitation (20%) and temperature (17%) during the reproductive stage explained large portions of G × E. However, trying to use environmental covariates to explain marker allele × E effects was less successful. For example, one marker (*Xbarc67*) × temperature during reproduction could explain only 2.6% of the total G × E for grain yield, yet it explained 76% of the total *Xbarc67* × E sums of squares. We wondered if these results reflect the complexity of understanding how genes interact with the environment, the relative simplicity of the environmental covariates (basically solar radiation, temperature, and precipitation, when compared to how the plant might have to integrate these variables biologically for evapotranspiration, physiological stresses, etc.)

The complexity of understanding G × E was later shown by Dhungana *et al.* (2007) who used structural equations (a generalized version of path analysis) involving marker alleles, environmental covariates, and intermediary/correlated and complex traits (in this case the components of yield and grain yield). Structural equation methodology is superior to factorial regression for decomposing complex relationships among traits. Using structural equation methodology was beneficial because it can elucidate the relationships between marker alleles and environmental covariates on intermediary traits (for example, the importance of increasing spikes per square meter) as they relate to the integrated trait of grain yield. Basically, the structural equation approach gave insight on how each marker affected all the components of yield at each phenological stage and what the marker allele aggregate effect was on the trait of interest, in this case grain yield. For example, Dhungana *et al.* (2007) found that the *Xbarc67* × temperature effect on the G × E for grain yield during the reproductive phase (see above) was due to higher temperatures in that phase being more favorable for the WI genotype at *Xbarc67* than CNN in terms of spikes per square meter. Compared to the findings of Campbell *et al.* (2004), these results demonstrated a deeper understanding of the yield G × E by showing that the effect of *Xbarc67* × temperature in the reproductive phase on yield G × E was partly due to its direct effect and partly due to its indirect effect via kernel per spike G × E and seed weight G × E. Thus the WI allele at *Xbarc67* affected grain yield by modifying spikes per square meter, seed weight, and grain yield directly and indirectly.

It is hoped that as we better understand the alleles that control important phenological events and agronomic traits, that this knowledge can be included into simulation models (e.g. Baenziger *et al.* 2004; Bertin *et al.* 2010). Simulation models have the potential to extrapolate information from measured environments to additional environments where the lines have not been tested and to help explain the complex interactions involved in G × E.

Current research

In our current research, we are trying to more precisely map the key chromosomal segments of 3A affecting grain yield in CNN (Ali, unpublished) and also validate the previously identified QTLs in CNN in a mirror image WI population (Mengistu, unpublished). Ali used 223 CNN(RICL3A)s developed using the monosomic method (Law 1966; Yen & Baenziger 1992) and doubled haploidy (Lizarazu *et al.* 1992; Jauhar *et al.* 2009) and 32 markers to precisely map the QTLs identified by Campbell *et al.* (2003). Phenotypic data was collected from 5 to 6 environments using four replications. In his research, he confirmed the two previously identified QTLs for grain yield and narrowed the region in which they were localized. In addition, he found an additional grain yield QTL expressed in one environment. Hence as more

RICLs, markers, and replications are used, we were able to identify QTL with smaller effects. As a goal of this research was to determine if grain yield is determined by numerous genes, each of which has a small effect and are virtually indistinguishable from each other, or by fewer genes, some of which have relatively larger effects; it seems the answer depends somewhat on the experimental design and how precisely you can identify small effects. The presence of genes with small effects is clear from the study of Buckler *et al.* (2009). In addition, while CNN(WI3A), CNN(WI6A), and CNN(WI3B) were significantly different from CNN and WI(CNN(3A) and WI(CNN6A) were significantly different from WI for grain yield, in reviewing the grain yield data from Berke *et al.* (1992a), 18 of the WI chromosome substitution lines in CNN background were higher yielding than CNN. Only three WI chromosome substitution lines in CNN background were lower yielding than CNN which is very unlikely to have occurred by chance alone if the substitution lines have the same mean yield as CNN. Similarly, 16 of CNN chromosome substitution lines in WI background were lower yielding than WI, while 5 CNN chromosome substitution lines in WI background were higher yielding than WI. Again this is very unlikely if there were no mean difference between WI and the lines.

Using 90 WI(RICL3A)s, 26 markers, and phenotypic data from 6 to 7 environments using incomplete block designs nested in 2 to 3 replications, Mengistu identified the major grain yield QTL previously identified by Campbell *et al.* (2003). This study showed the CNN-allele reduced grain yield in the WI background and was localized at the same region as the favourable allele in the CNN(RICL3A)s. Hence the CNN(RICL3A)s and WI(RICL3A)s were truly mirror image populations of each other.

We were also interested in knowing if other useful alleles for improving Nebraska wheat germplasm might be found in modern germplasm from Turkey. Nebraska and Turkey share some of the same climatic features and we thought it that useful alleles might be found in Turkish wheat cultivars that U.S. breeders have not successfully incorporated into their germplasm. Auvachanon (unpublished) compared, using genetic similarity or distance estimates, 23 Nebraska wheat cultivars to 22 Turkish wheat cultivars at the molecular level and also phenotypically for agronomic and end-use quality performance. In general, at the molecular and phenotypic level, the historic Nebraska wheat cultivars clustered with many of the Turkish wheat cultivars. However, modern Nebraska and Turkish wheat cultivars tended to cluster in groups based on their country of origin. A few Turkish cultivars clustered (based on molecular and phenotypic data) with modern Nebraska wheat cultivars and are currently being used in crosses to determine if they may have useful alleles.

Our work has also stimulated development of new methodological approaches. Mi (unpublished) developed a Bayesian multi-trait QTL mapping approach capable of incorporating causal structure among traits. The approach is based on a mixture structural equation model, which allows researchers to decompose QTL effects into direct, indirect, and total effects. Results indicated, that compared to previously used approaches, the method improved the statistical power of QTL detection, accuracy, and precision of parameter estimates but also provided important insight into how genes regulate traits directly and indirectly by fitting a more biologically sensible model. In addition, Mi (unpublished) developed QTL software that allows researchers to incorporate any causal structure among traits and allows for a wide variety of independent variables and covariance structures that maybe used to model many different genetic, environmental, and field effects.

Future work

The ultimate goal of this research is to understand the genetic basis of grain yield. To do this we will need to incorporate the tools of modern genetic analysis and hopefully eventually indentify and clone the genes affecting grain yield. As such, we have continued to develop populations suitable for fine mapping the QTLs on chromosome 3A. Over 900 CNN(RICL3A)s have been developed from crosses involving CNN(RICL3A) × CNN where the RICL has the segment of interest for higher grain yield. Epistasis also needs to be studied in wheat and we hope to use doubled haploid technology to understand how chromosome 3A interacts with chromosome 6A. Basically we will make doubled haploids from the F_1 of CNN(WI3A) × CNN(WI6A) and WI(CNN3A) × WI(CNN6A). This research will be greatly helped by developing a physical map (e.g. Dilbirligi *et al.* 2006) and sequencing of chromosomes 3A and 6A.

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